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A TEXT-BOOK OF DENTAL ANATOMY AND PHYSIOLOGY

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BY

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PREFACE

Science is indebted to Sir Richard Owen for the foundation of the study of Odontology, for as early as the year 1845 he published his remarkable work in two volumes entitled *Odontography ; A Treatise on the Comparative Anatomy of the Teeth*, the result of exhaustive studies of the forms and structure of the teeth of fishes, reptiles and mammals. This has been the foundation upon which all subsequent investigations have been based. Sir Charles Tomes followed with his masterly work on Dental Anatomy, which ever since has constituted the student's *vade mecum*. During the last twenty years numerous books on the subject have appeared in Europe and America, and at the end of this volume is printed a list of some from which the authors have derived information.

Most of the books, however, are designed for the use of students of Zoology ; and the authors trust that there may still be room for this small, condensed text-book, which is intended to meet the requirements of dental students preparing for their examinations, and is based on the curricula of the various licensing bodies. To fulfil this purpose, it is felt that ample illustration is of the first importance. The bulk of the illustrations are new, and are from specimens collected and prepared by the authors.

The authors are greatly indebted to Sir Arthur Keith, Messrs. J. and A. Churchill, Messrs. Henry Frowde and Hodder and Stoughton, and Messrs. Edward Arnold & Co. for permission to make use of illustrations which are acknowledged elsewhere in this book. Dr. Humphrey Humphreys, M.D.S., has given very valuable assistance and advice, especially in regard to Chapters I and XX, for which the authors are grateful.

Thanks are also due to the Council of the International Dental Congress for permission to make extracts from the

Transactions for 1914 ; to Mrs. West for kindly allowing the reproduction of sketches of the teeth of venomous snakes, made by her late husband, Professor G. S. West ; to Miss Nellie Carter, D.Sc., and Mr. E. Hoermann for their accurate drawings, and to Mr. Sydney Pitcher of Gloucester for some of the photographs with which the book is illustrated.

The original photomicrographs illustrating the histological section of this work were done, some by the late Mr. Cox, of the Zoological laboratory of the Birmingham University ; some by Mr. Brailsford, of the Birmingham University ; the three camera lucida drawings are by Dr. Nellie Carter, and the remainder by Mr. A. W. Wellings.

We desire to express our grateful thanks to Professor Shaw Dunn, formerly Professor of Pathology in the University of Birmingham, for the use of the photomicrographic apparatus and for much valuable help and assistance (the photograph of the dentinal fibrils in their tubules, longitudinal section, was taken by him) ; also to Professor E. Wace Carlier, Professor of Physiology in the University of Birmingham, for the use of his Histological laboratory and for much advice in details of histological technique ; and to Mr. J. Howard Mummery for permission to reproduce some of his illustrations of dental histology.

J. H.
A. W. W.

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PART I

DENTAL ANATOMY

CHAPTER I

THE DEVELOPMENT OF THE JAWS

Early Development of the Head Region

The first few weeks of fœtal life see the fertilized ovum develop, first by segmentation or division and then by differentiation of its cells into the primitive embryo. The most striking of the changes involved is the development of the segmenting ovum from a solid cluster of cells into a vessel enclosing a cavity. This cavity represents the primitive gut, and a section taken through the ovum in this early stage shows that its walls consist of three layers of cells : an inner layer lining the cavity —the entoderm or hypoblast ; an outer layer forming the "skin" of the developing ovum—the ectoderm or epiblast ; while between these two there appears at an early stage an intermediate layer—the mesoderm or mesoblast. This early differentiation of the cells into three layers is important, as it is possible to trace to each of them the origin of the different organs and tissues of the body.

It may be said in general terms that from the ectoderm is developed the epithelium of the skin and all structures derived from it such as hair, nails and the enamel of teeth : to these must be added the whole of the nervous system both central and peripheral. Very early a deep furrow appears on the surface of the embryo in the dorsal position and deepens till its edges meet and fuse : it is then separated from the surface by the growth of mesoderm and becomes a hollow tube (the neural canal) lying embedded in the latter tissue. From it are developed the brain, spinal cord and peripheral nerves, the cavities of the two former remaining as evidence of its

tubular origin. For this reason the odontoblast cells of the dental pulp, which are mesodermal in origin, cannot be regarded as nerve cells. From the endoderm is developed the epithelium lining the alimentary and respiratory tracts, together with the glands that open into them, such as the liver and pancreas, while from the mesoderm are developed the remaining organs and tissues of the body, such as the connective tissues, the muscles, the vascular system and the urino-genital system.

As the ovum develops into the embryo, attention must be confined to the head region where interesting developments take place. A longitudinal section taken at the end of the second week (Fig. 1) shows the primitive gut, with mesoderm all round it, and at its tip a thin membrane still separating it from the outside, the bucco-pharyngeal membrane. The position of this membrane is marked on the surface by a deep pit, the stomatodeum, which in the third week, when the membrane shrivels up and disappears, becomes part of the alimentary canal. The entrance to this canal is therefore lined with ectoderm, and the junction between the two, i.e. the original position of the bucco-pharyngeal membrane, is marked by an oblique plane from the back of the lower teeth to the roof of the pharynx. The enamel of the teeth is thus derived from ectoderm, not from endoderm.

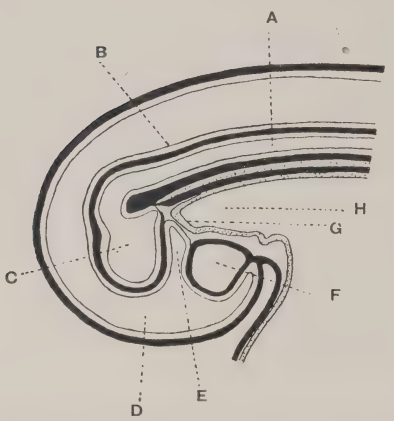


FIG. 1.—Longitudinal section through the head of an embryo at end of second week.

A, Neural canal; B, cranial capsule or surface of embryo; *c*, fore-brain; *D*, amniotic cavity surrounding the embryo; *E*, stomatodeum; *F*, cardiac area; *G*, bucco-pharyngeal membrane; *H*, primitive fore-gut.

Visceral Arches.—At about the end of the first month the lateral and ventral walls of the fore-gut are strengthened by five curved arches on each side, separated from one another by deep clefts. These are the visceral arches, and the first of them forms a kind of rim to the entrance of the alimentary canal. They resemble, and are indeed strictly homologous

with, the gill arches and gill clefts of fish, but in the mammalian embryo they begin to fuse with one another early and the clefts disappear. The external and middle ears remain as a relic of the first cleft, while the first arch contributes to the development of the jaws.

If at this stage we take a front view of the embryonic head region (Fig. 2, A), we shall see that there is as yet no face. The simple opening of the primitive gut is bounded above by the brain laterally and below by the first visceral arch, while to either side of it the eyes are beginning to develop. Late in the

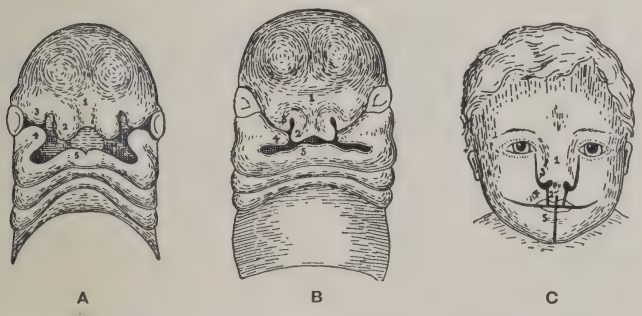


FIG. 2.—A, Head of embryo end of 1st month; B, Head of embryo middle of 2nd month; C, Head of child showing embryonic fissures.

1. Median nasal process; 2. Globular process; 3. Lateral nasal process; 4. Maxillary process; 5. Mandibular process.
A and B after Cunningham, by kind permission of Messrs. Frowde and Hodder & Stoughton. C from Mills & Humphreys' text-book of Surgery, Edward Arnold & Co., by permission.

first month, however, certain processes grow in from the sides of the opening which fuse together about the middle of the second month, and divide it into three separate orifices, two nasal and one oral. From the upper margin grows a large central process —the median nasal process which divides near its tip into two small globular processes; and two smaller processes at either side—the lateral nasal processes. From the lateral margins of the opening the maxillary processes grow inwards on either side. The way in which these processes meet and fuse together is best comprehended by a comparison of Figs. 2 (B) and 2 (C): from these it will be clear that the median nasal process forms the septum of the nose and the globular processes the premaxillæ and central portion of the upper lip: the lateral nasal processes form the sides and alæ of the nose: the maxillary processes form the maxillæ, the cheeks, and the lateral portions of the upper lip: while the ventral portion of the first visceral arch,

or mandibular process as it is often called, forms the lower jaw, lip and cheek.

Oral and Nasal Cavities.—It has been said that the growth and fusion of these processes divide the simple opening into the gut into two nasal and one oral *orifice*. The further division into oral and nasal *cavities* is effected as follows. The median nasal process sends a vertical plate backwards to form the septum of the nose, and to meet it the maxillary process sends a horizontal process inwards to form the palate : when the three meet and fuse the formation of oral and nasal cavities is complete.

Under certain conditions fusion of these processes may be incomplete and congenital defects occur. The commonest of these are hare-lip and cleft palate, conditions which result from a partial or complete lack of fusion between the median nasal process with its offshoots, the globular processes and septum, on the one hand, and the maxillary processes with their offshoots, the palatal processes, on the other. But for a description of these and other malformations of the head region the reader is referred to a text-book of surgery.

Growth of the Upper Jaw

The maxilla, having taken its shape in soft tissue as above described, in the first part of the second month of fœtal life begins to ossify in the second part of the same month. The primary centre of ossification is in the neighbourhood of the canine tooth-germ, and from this single centre ossification spreads rapidly in all directions, enclosing the dental nerves in bony canals. The bone is developed chiefly in membrane, though a secondary or metaplastic cartilage appears for a time on the outer or malar surface, which is soon converted into bone.

The premaxilla is ossified from two centres, the greater part, including the region around the incisor tooth germs, being developed from the palato-facial centre, while a small portion above and behind is developed from a separate centre, the sub-vomeran. Bony union between the premaxilla and maxilla occurs at birth in man, though the suture is visible till the third year. In the anthropoid apes this union is delayed in order that growth may take place at the suture sufficient to

accommodate the large permanent canine tooth. In the chimpanzee union takes place as soon as that tooth is erupted, but in the gorilla and orang-outang the suture remains open throughout life.

The Growth of Bone.—We have now to consider the growth that takes place after birth subsequent to the complete ossification and fusion of these bones. Though "interstitial growth" is described by some authors, it is difficult to conceive how this can take place in an unyielding and rigid tissue like bone; and there can be little doubt that growth here, as in membrane bones elsewhere, consists of a deposition of bone by osteoblasts on the surface towards which the bone is growing, accompanied by a removal of bone by osteoclasts on the surface *away from which* growth is proceeding. In the case of a hollow bone like the maxilla the case is not at all unlike that of "expansion" of bone (so called) by a cyst, as its growth is largely governed by the expansion of the maxillary antrum. At birth this is represented by a small shallow depression on the lateral surface of the nose and the tooth germs are only separated from the orbit by a thin plate of bone. But as the antrum grows the bone is "expanded" by the double process of deposition and absorption of bone until the teeth come to be separated from the orbit by the whole depth of that cavity.

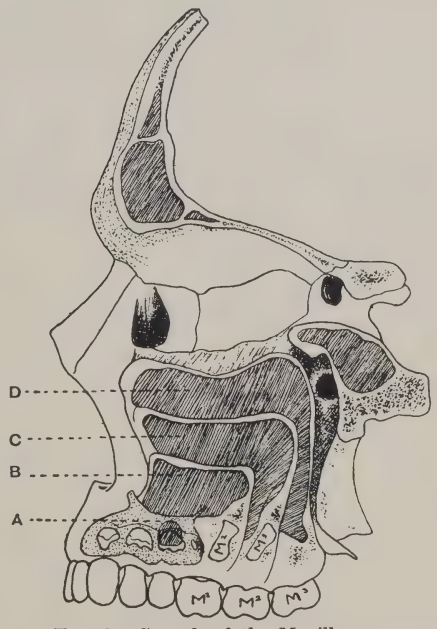


FIG. 3.—Growth of the Maxilla.

A, The stippled portion represents the maxilla at birth, the shaded portion being the antrum; *B*, antrum at 9th year; *C*, antrum at 15th year; *D*, antrum of adult.

For convenience of representation the premaxilla is taken as the fixed point (natural size) (after a drawing by Sir Arthur Keith).

The process is well shown in Fig. 3 (after Keith), which represents four stages in the growth of the antrum and upper jaw. It shows also how the growth of the antrum governs the eruption of the permanent molars, the crowns of which are at first directed backwards, the expansion of the antrum rotating them till they reach a vertical position. For purposes of representation the premaxilla is taken as the fixed point and the antrum and jaw appear to grow upwards and backwards. But it should be clearly realized that in the body the fixed surfaces of the maxilla are above where it articulates with the frontal bone, and behind where it articulates with the palate bone. So that its own intrinsic growth thrusts it downwards from the floor of the orbit and forwards from the pterygoid process. To summarize, therefore, the development of the maxilla it may be described as growing in three directions :—

I. *The downward growth* of the body and of the alveolus must be considered separately. That of the body has already been described in its relation to the expansion of the antrum. It is most marked posteriorly in the molar region. Thus according to figures published by Keith, the depth of the upper jaw, measured from the fronto-maxillary suture to the edge of the central incisor, increases from 30 mm. at birth to 70 mm. in the adult (an increase of 133·3 per cent.), while the posterior depth measured from the floor of the orbit to the alveolar margin grows from 10 mm. at birth to 40 mm. in the adult (an increase of 300 per cent.).

The alveolar portion of the bone grows downwards with the eruption of the teeth and is absorbed when these are shed. This applies to both dentitions, and it is therefore a structure of a more temporary nature than the body of the bone.

This downward growth of the maxilla is probably the governing factor in the elongation of the ascending ramus of the mandible and the decrease in its angle ; the reasons for these changes will be described presently.

II. *The backward growth* of the maxilla is also governed by the expansion of the antrum and provides room for the eruption of the molar teeth. But owing to its articulation behind with the palate bone the effect of this backwards growth is to push the whole bone forwards. Thus, although no intrinsic growth of the bone takes place in a forward direction, the

lower portion of the face is much more prominent in the adult than in the infant.

III. *The outward growth* of the maxilla again affects both the body and the alveolus. In the body its effect is to push the malar bones outwards and increase the prominence of the cheeks. The alveolus is to a limited extent thickened on the labial and buccal surfaces when the permanent teeth erupt, so that a line along its centre represents a curve of larger radius than when the deciduous teeth are standing. This

Fig. 4.—Lower jaw of a ninth month's fœtus superimposed upon an adult jaw, to show in what directions increase has taken place (after Tomes).

Reproduced by permission of Messrs. J. & A. Churchill from Tomes' *Manual of Dental Anatomy.*

accounts for the somewhat greater arc of the permanent as compared with the deciduous teeth.

No noticeable growth of the maxilla takes place either upwards, forwards, or inwards. Inward growth is clearly impossible, as it articulates with its fellow maxilla in the middle line. And the curve marking the palatal surface of the alveolus is found to be the same in the infant and the adult, save that of course in the latter it is prolonged further backwards.

Growth of the Mandible

The mandible is formed from the ventral portion of the first visceral arch or *mandibular process*. Each visceral arch contains a cartilage, an artery, a nerve, and a muscle. The cartilage of the first visceral arch is known as *Meckel's cartilage*, and is thus the forerunner of the lower jaw, though its dorsal end also forms two of the auditory ossicles, the malleus and the incus. The mandibular nerve represents the main nerve of the first visceral arch.

The mandible is the second bone in the human body to ossify, being preceded only by the clavicle. A centre for each half appears at the sixth week near the mental foramen in the membrane surrounding Meckel's cartilage and spreads around the mandibular nerve and its branches, enclosing Meckel's cartilage as it forms. The bone is therefore primarily a membrane bone, though eventually ossification invades Meckel's cartilage, which disappears except for the malleus and incus. At a comparatively late period secondary or metaplastic cartilage appears in certain positions on the developing bone, at the condyle, at the anterior margin of the coronoid process, and on the top of the alveolus in the incisor region : this latter cartilage sends a process downwards along the symphysis. All these metaplastic cartilages are eventually invaded by ossification from the membrane round them and disappear, though possibly the small ossa mentalia sometimes found in the region of the symphysis may represent an independent ossification of the symphysial cartilage.

At birth the two halves have still only a ligamentous attachment at the symphysis, and bony union does not take place there till the eighth month after birth.

Growth of the Bone.—As regards postnatal growth of the bone, the remarks on growth of the maxilla apply with equal force here. No proof of interstitial growth exists, and it is difficult to conceive how such growth can occur. The chief and probably the only process concerned is an osteoblastic deposit of bone on the surface towards which the bone is growing, accompanied by an osteoclastic absorption of the surface away from which growth is proceeding. In describing the growth of the bone it is necessary to select some fixed point which remains in much the same position throughout, and

following Tomes we may choose the genial tubercles, the inferior dental canal, and the mental foramen. The latter opening being oblique necessarily moves a little forward and upwards as the bone is thickened from the outside, but such alteration is slight and may be allowed for. With this proviso the three points do not appreciably change their relative positions and give us a fixed base from which to estimate the increases in the size of the bone.

The difference between the alveolus and the body of the bone needs to be borne in mind even more constantly than in the case of the maxilla. For in the latter the alveolus is a relatively small portion of the bone, while in the mandible at birth it constitutes the greater portion of it. For convenience of description growth in the different directions may be taken separately and reference to the accompanying figures (Figs. 5, 6 and 7) will illustrate their meaning.

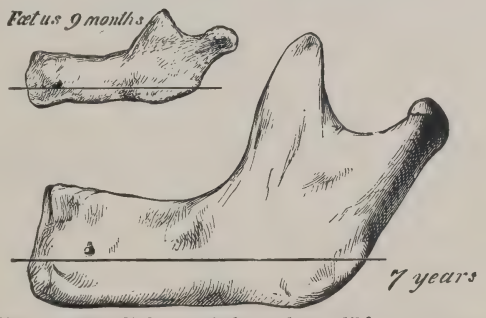


Fig. 5.—Mandible at birth, and mandible at 7 years. (After Tomes.)

I. Backward Growth.—At birth the crypt of the second milk molar lies immediately to the front of the ascending ramus, and it is obvious that room can only be made for the eruption of the permanent molars by bodily removal of the ascending ramus backwards. This is effected by the absorption of bone from the front of the ramus, and coincidently its deposition behind. Similarly bone is constantly being removed from the front and deposited on the back of the coronoid process and condyle, and this process goes on up to the eruption of the third mandibular molar. Thus the internal oblique line on the ascending ramus represents the series of positions which the condyle has occupied during the growth of the bone.

II. Upward Growth of the ascending ramus goes on concurrently with its backward displacement, and with this upward growth occurs a decrease in the angle the ascending ramus makes with the body of the bone. At birth the ramus

is so short that the condyle stands on a level with the alveolus and the angle it makes with the body is about 135°. In adult life the ramus has grown upwards and makes an angle with the body of 110–20°, while in old age, when the teeth are lost, a partial return to the condition of infancy occurs. The ascending ramus then becomes shorter and more slender, while the angle it makes with the body is more obtuse. These changes may be looked upon as compensatory to the downwards growth of the maxilla. It will be remembered that this is most marked in the molar region and it therefore pushes against the occlusal surface of the lower molars. Unless compensating changes took place in the mandible the mouth would be forced permanently open and only the last molars would be in contact. (This condition actually occurs in cases of arrested development of the mandible). If complete occlusal contact of the teeth is to be maintained the ramus of the mandible must obviously lengthen step by step with the downwards growth of the maxilla, and as the latter growth is vertical so will the ramus become more nearly vertical in relation to the body of the lower jaw. Again, in old age when the teeth are lost occlusal contact is lost altogether, and in the effort to regain it the ramus becomes somewhat shorter and the angle of the jaw increases until the bare gums can meet. The wearing of dentures will tend to retard these changes. Muscular wasting also and the loss of teeth, by reducing strain on the bone, encourage osteoclastic absorption, and all the proportions of the senile bone become more slender.

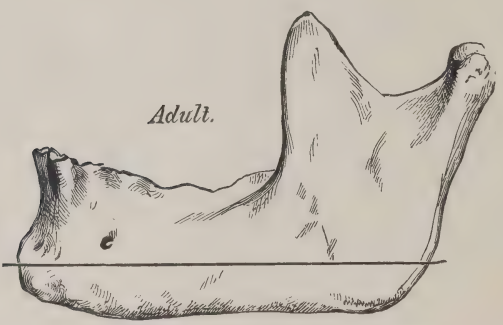


Fig. 6.—Mandible of adult (after Tomes).

Upward growth of the body and horizontal ramus is confined to the alveolus. When the teeth of either dentition erupt, the alveolar process is built up around their roots to be absorbed when the teeth are lost. Finally in the edentulous jaw of

advanced age the alveolus is so completely absorbed that the mental foramen comes to lie at the upper margin of the bone.

III. Downward Growth.—Fig. 5 shows that considerable downward growth of the body of the mandible below the inferior dental canal takes place from birth to the seventh year of life. After that time little or no increase takes place in this direction.

IV. Forward Growth is slight and is due partly to the thickening of the mandible by deposit of bone on its outer surface which goes on until adult life is reached, and partly to the special development of the chin and mental prominence. This first becomes noticeable about the sixth month after birth and slowly increases up to adolescence.

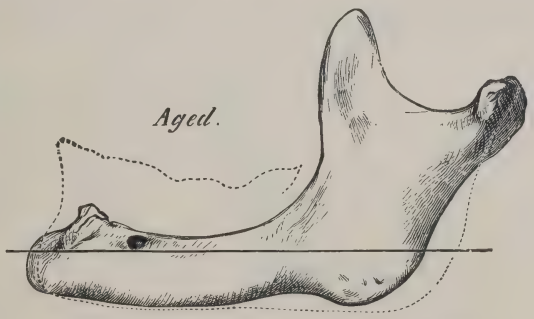


Fig. 7.—Lower jaw of an aged person, the dotted lines indicating the outlines of the parts removed by absorption as the jaw assumes the form characteristic of old age.

Figs. 6 and 7 are reproduced from Tomes' *Manual of Dental Anatomy*, by kind permission of Messrs. J. & A. Churchill, 7 Great Marlborough Street, London.

V. Outward Growth is due to the continuous deposit of bone beneath the periosteum and results in great strengthening of the bone. Owing to the obliquity of the mental foramen this results in shifting of this orifice forwards and upwards, and if the outer surface of an adult jaw is rasped down till it is reduced to its thickness in infancy the foramen will be seen in its original position. This happens naturally in the wasting of the bone produced by old age.

Outward growth of the alveolus is similar both in its nature and its effects on the eruption of the teeth to that of the maxilla previously described.

Growth of the bone therefore takes place in every direction except inwards. Growth in that direction would obviously encroach on the tongue, and Fig. 4 shows that the inner surface of the bone has precisely the same curve in the infant and the adult.

CONDITION OF JAWS AND TEETH

Salient dates in the development of the jaws, eruption and calcification of the teeth.

Eruption of Temporary Dentition

(1) Sixth month before birth.

At this early date calcification of the developing tooth germs commences, and is well seen in the forming enamel and dentine.

(2) Birth.

(*a*) *Condition of Jaws.*—The premaxilla at birth unites with the maxilla. The two halves of the mandible are united by fibrous attachment, the ascending ramus is at a level of 135° to the body of the jaw, and the condyle on a level with the alveolar portion.

Fig. 8.—Mandible at birth.
C, Canine.

(*b*) *Condition of Alveolus.*—The developing teeth, surrounded by their dental follicles, lie in open crypts, the walls of which are forming in the front of the jaw. At this stage if the gum be stripped off the tooth germs come away with it, leaving the crypts of bare bone; at the back the jaw is in the condition of an open gutter, without partitions.

In a dried specimen the teeth will fall out of their sockets, but later on towards the 3rd month the edges of the crypts close in over the developing crowns and conceal them.

(*c*) *Calcification of Teeth.*—At this stage half the crowns of the central and lateral incisors are formed, the tips of the canines, the surface of the crown of the first molar, and the cusps and dentinal portion of the crown of the second molars. The antrum is merely a depression in the side of the nose.

(3) Eighth month.

(*a*) *Condition of Jaws.*—At this period rapid development occurs, the two halves of the lower jaw are united at the

symphysis, and the chin is first visible, sockets for the teeth are fully formed, and a crypt for the first permanent molar.

(*b*) *Eruption of Milk Teeth.*—The cutting of the milk teeth commences. The mechanism by which this is brought about is unknown, notwithstanding the numerous theories on the subject (*see* Chapter III).

Rapid absorption of the walls of the crypts begins at this stage, allowing the crowns of the teeth to pass through the wide openings and move upwards. Afterwards the bone is re-deposited around the necks of the teeth forming ultimately the alveolar sockets, which as the roots elongate are moulded to them.

After this period the eruption of the milk teeth goes on

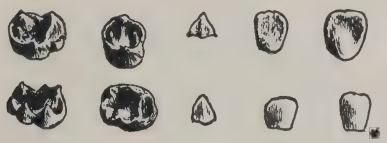


Fig. 9.—Crowns of milk teeth at birth.

intermittently, the teeth being cut in groups, a stage of activity being followed by long intervals of rest.

(*c*) *Calcification.*—(i) The calcification of the crowns of the milk teeth is now practically complete.

(ii) In the permanent teeth the tips of the incisors and canines, and the masticating surfaces of the first molars, are calcified.

(4) End of second year.

Eruption.—The eruption of the milk dentition is now completed, although the roots are not fully formed until some time afterwards.

(5) Teeth at fifth year.

Calcification.—In the permanent teeth the crowns of incisors and first molars are almost complete; the canines, three-quarters of the crowns; the cusps of the premolars and second molars.

Fig. 10, from which the outer alveolar plate has been removed, shows the upper jaw at six years, with all the milk teeth in position: behind the incisors are foramina, through each of which passes the gubernaculum, a thin

cord of fibrous tissue, which penetrates to the tooth sac of the permanent tooth below, to which it is attached. The first permanent molar is just emerging into position, from its widely-open crypt.

At this stage the crown of the second permanent molar lies at the back, and far beneath its neighbour, almost concealed in its socket, only the dentinal surface being complete, the summit of the crown facing the back of the mouth, and deep below it is the germ of the third molar.

During the growth of the jaw backwards these last two molars, with their crypts, will be gradually carried upwards until the crowns reach the line of occlusion.

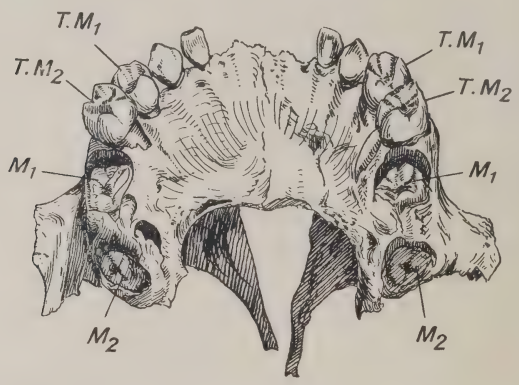


FIG. 10.—Upper jaw at 4 years. Temporary molars in position ; permanent molars in crypts, the second permanent molar being deeply embedded. The surface of the crown of the first permanent molar is formed and the alveolar crypt is widely open. The coronal portion only of the second permanent molar is shaped.

ERUPTION OF PERMANENT TEETH

(6) Teeth at seventh year.

Eruption.—At the commencement of the 7th year the jaws show signs of the approaching eruption of the permanent teeth.

The teeth in front are becoming separated by the widening jaw, the incisors and canines standing well in front of their permanent successors. The jaws contain all the milk teeth, and the permanent dentition in various stages of development. Previous to the eruption of the permanent teeth absorption

of the roots of the milk teeth commences by the action of absorbent cells. The cementum is usually the first to be attacked, followed by the dentine, and in time even the enamel is affected. Tomes considers that "the absorption is independent of pressure." The osteoclasts excavate the substance of the tooth so thoroughly that frequently only the enamel part of the crown remains.

A study of the jaws and teeth at this age is illuminating.

Upper Jaw or Maxilla.—*Central Incisors.*—The crown is formed and a small portion of root, the teeth being wide apart at the base converge as they descend in an oblique fashion, the biting edges are serrated as in all the incisors.

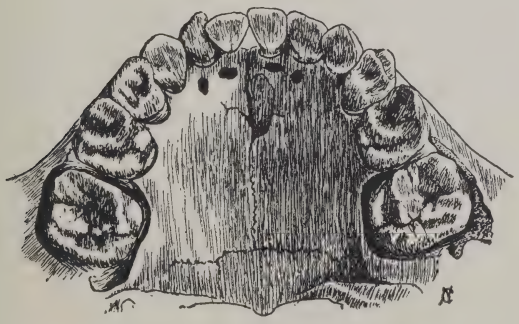


FIG. 11.—Upper jaw at 6 years.

Lateral Incisor.—The crown only is formed, and lies somewhat behind the centrals.

Canine.—The crown only is formed, and lies high up underneath the orbit, ultimately descending between the lateral incisor and the developing crown of the first premolar, which at this stage lie closely together.

Premolars.—The premolar crowns are concealed in crypts between the divergent roots of the milk molars, the first premolar being more calcified than the second.

Molars.—The first permanent molar is in position, but the apices of the roots are not yet complete. Behind it lies the hollow crown of the second permanent molar, partly calcified, enclosed in its crypt, and facing the back of the mouth, while the third molar is still in its germ stage, in a slight depression in the bone.

Lower Jaw or Mandible.—The same characteristics apply largely to the lower jaw.

Central Incisors.—These teeth are formed, except the apices of the roots ; they stand in front of the lateral incisors, and their serrated biting edges project beyond the alveolus.

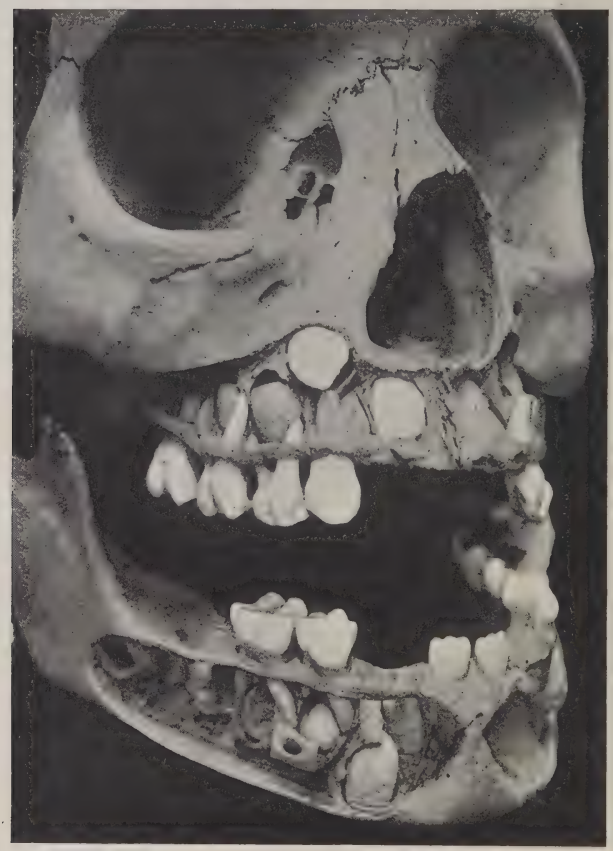


Fig. 12.—Developing teeth at 7 years.

Lateral Incisors.—The roots of these incisors are not so complete as those of the central incisors, and the crowns are partly overlapped by the central incisors and canines.

Canines.—The crowns are complete and stand in front of the lateral incisors, giving a square appearance to the jaw.

Premolars and *Molars.*—The same description applies to

them as to those in the upper jaw, but in eruption the lower first molar comes into position slightly before the corresponding upper tooth, guided and adjusted into place by

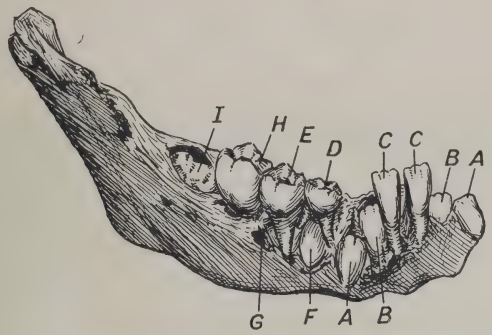


Fig. 13.—Right side of mandible towards end of 6th year.

A A, permanent canines ; *B B*, lateral permanent incisors ; *C C*, central permanent incisors ; *D*, first temporary molar ; *E*, second temporary molar ; *F*, crown of 1st premolar ; *G*, crypt of 2nd premolar ; *H*, first permanent molar ; *I*, crown of 2nd permanent molar in crypt.

occlusion, with the distal portion of the occlusal surface of the crown of the second upper milk molar, which in closing extends beyond its fellow in the lower jaw.

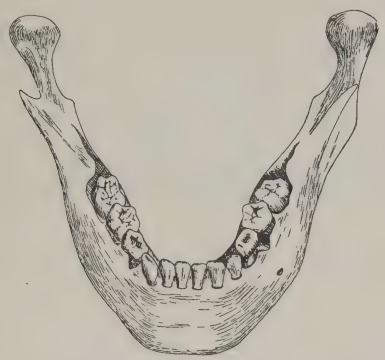


Fig. 14.—Lower jaw at 6 years.

(7) Teeth at twelfth to fourteenth year.

The eruption of the permanent teeth is now complete, with the exception of the third molar, which is usually erupted in early adult life, though the crown is now calcified.

When a tooth erupts only a portion of the root is formed. It is completely calcified about one year after eruption in the milk teeth, and about three or four years after eruption in the permanent teeth.

Order of Eruption of Teeth

(*a*) *Milk Teeth.*—The process of eruption commences at

Fig. 15.—Dentition at 9 years. Showing upper and lower permanent incisors, and first permanent molars erupted, with temporary canines and molars still in place. Upper permanent canines are high up beneath the orbit.

about the 6th month, ending at the close of the 2nd year. The approximate dates are as under—

1. Lower central incisors,
2. Four upper incisors,

} 5th to 10th month.

3. Lower laterals and four first molars, 12th to 14th month.
4. Four canines, 14th to 20th month.
5. Four 2nd molars, 20th to 30th month.

(*b*) *Permanent Teeth.*—The eruption of the permanent teeth extends from the 7th to the 12th years, excepting the 3rd molars, which are erupted much later. The order of eruption varies considerably. Usually the lower teeth appear before the upper, and the teeth of females before those of males. The approximate dates and order appear below.

Fig. 16.—Skull of child of 10½ years, showing position of molars. First molar erupted and in occlusal line. Second molar with crown just emerging from crypt. Third molar deep down, with crown facing backwards.

1. First permanent molars	7	years.
2. Central incisors	7 to 8	,,
3. Lateral incisors	8 to 9	,,
4. First bicuspids	10 to 11	,,
5. Canines	11 to 12	,,
6. Second bicuspids	11 to 12	,,
7. Second molars	12 to 13	,,
8. Third molars	Adult period.	

The process of eruption is similar to that in the milk dentition ; absorbent cells attack both the roots and alveolus,

providing a large orifice for the passage of the succeeding tooth, which, when in position, is secured, and the socket formed by further alveolar growth, adapting itself to the growing roots. The symmetrical arrangement of the teeth depends upon—

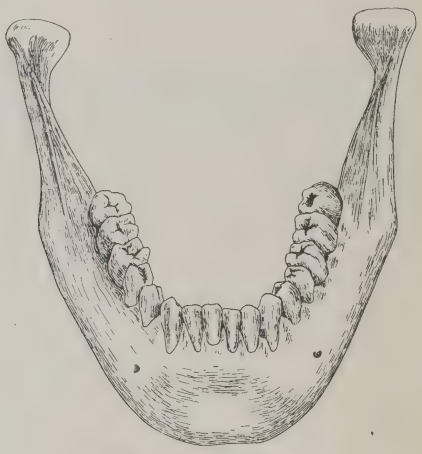
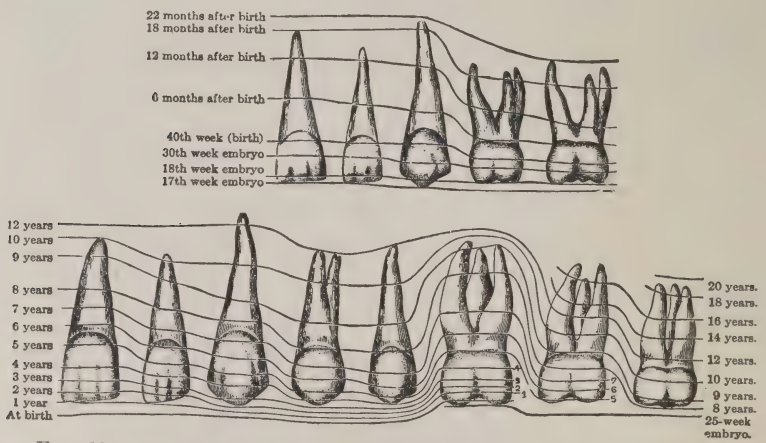


FIG. 17.—Lower jaw of adult.

(1) Position and shape of body of the jaws.
(2) Pressure of lips and cheek.
(3) Pressure of tongue.
(4) Occlusion.



FIGS. 18, 19.—From Kirk's *Operative Dentistry* (Figs. 115, 116) to illustrate the progress of the calcification of the teeth.

CHRONOLOGY OF HUMAN TOOTH DEVELOPMENT

(*Adapted from Rose's Table*)

Pre-Natal Development

Length of embryo	*Age*	
12–15 mm.	30–40 days	Primary epithelial inflection. First trace of Meckel's cartilage—no bone.
17 mm.	48 days	The primary epithelial inflection has divided into the "lip-furrow" band and the tooth-band. The deepest layer of the epithelium is cylindrical. Meckel's cartilage complete —first traces of bone.
2·5 cm.	9 weeks	Tooth-band shows alternate enlargement and depressions.
3·2 cm.	10 weeks	Enamel organs club-shaped, 8 dentine papillæ present.
4 cm.	11½ weeks	10 papillæ for the deciduous teeth present in each jaw. Deepening of the lip groove.
11½ cm.	14 weeks	The tooth germs of the deciduous teeth lie against the side of the tooth-band like swallows' nests. First appearance of stellate reticulum. The tooth-band grows beyond the last milk molar without a vertical connection as yet with the surface epithelium.
18 cm.	17 weeks	The necks of the enamel organs of the anterior teeth have become attenuated. Those of the molars are still broad. The tooth-band is irregularly thickened and fenestrated in front. The dental groove appears in front of the mouth. The dentine papilla of the first permanent molar appears.
24 cm.	20 weeks	Dental groove extends to the back of the mouth. Calcification in the incisors commences. Trace of tooth-sac of 1st permanent molar.
30 cm.	24 weeks	Fenestration of tooth-band anteriorly. Commencement of calcification in deciduous canines and molars. Papillæ of permanent incisors embraced by enamel organ. Appearance of papilla of permanent canines. Enamel organ of first permanent molar fully developed.

Length of embryo	*Age*	
36 cm.	29 weeks	Calcification in each cusp of deciduous molars, but cusps not yet united. Appearance of tooth sacs of permanent incisors and canines. Tooth-band thickened for 1st premolar.
40 cm.	33 weeks	Cusps of deciduous molars united, enamel organ of 2nd premolar, no calcification in 1st permanent molar as yet.

Post-Natal Development

Deciduous dentition.

At birth,		Length of tooth calcified
9 months fœtus	Incisor 1	4·5 mm.
	Incisor 2	4 mm.
	Canine	2·5 mm.
	Molar 1	2·5 mm.
	Molar 2	3 mm.

Permanent dentition.

Only the caps on the cusps of the first permanent molar are calcified.

4 months

Deciduous dentition.

Incisor 1	whole of crown and ·5 mm. of root
Incisor 2	5 mm.
Canine	5 mm.
Molar 1	4·5 mm.
Molar 2	3–4 mm.

Permanent dentition.

Molar 1	4 cusps and 1–2·5 mm. of crown
Molar 2	1st appearance of enamel organ

6 months

Deciduous dentition.

Incisor 1	3·5 mm. of root
Incisor 2	1·5–2·5 mm. ,, ,,
Canine	0·5 mm. ,, ,,
Molar 1	4–5 mm.
Molar 2	3–4·5 mm.

6 months

Permanent dentition.

Incisor 1	3 mm.
Incisor 2	2·5 mm.
Canine	1 mm.
Molar 1	2–3·5 mm.
Molar 2	papillæ

2 years

Deciduous teeth generally all erupted, but their roots are not yet complete.

In the second permanent molars the 4 cusps are formed and 1·5–2 mm. of the crown.

3¼ years

Deciduous dentition.

	Length of tooth calcified
Incisor 1	11 mm. of root
Incisor 2	11 mm. ,, ,,
Canine	11 mm. ,, ,,
Molar 1	8–9 mm. ,, ,,
Molar 2	6–7 mm. ,, ,,

Permanent dentition.

Incisor 1	Crown complete
Incisor 2	7 mm. of crown
Canine	8–9 mm. of crown
Premolar 1	Cusps united 5–6 mm. of crown
Premolar 2	Cusps separate 1–2·5 mm.
Molar 1	1·5 mm. of root
Molar 2	2 mm. of crown
Molar 3	Enamel organ appears

5 years

The papillæ for the third permanent molars appear.

CHAPTER II

MACROSCOPIC ANATOMY OF HUMAN TEETH AND THE TEMPORO-MANDIBULAR ARTICULATION

Permanent Dentition

Number.—The dentition of man is expressed by the formula i. $\frac{2}{2}$, c. $\frac{1}{1}$, p.m. $\frac{2}{2}$, m. $\frac{3}{3}$, total 32. Man has lost a pair of incisors and two pairs of premolars in each jaw.

Arrangement.—Man's teeth, unlike those of any living anthropoid, are arranged in a sweeping curve, widening towards the back of the molars, all are in series, there are no interspaces, each tooth touches the crown of its fellow, and no tooth is raised above the others. Man no longer requires teeth to

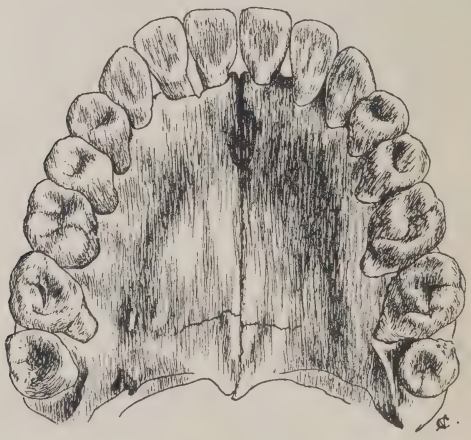


Fig. 20.—Human upper teeth, adult.

grasp and tear his food, or for weapons of offence and defence; they are now needed only for slicing and crushing or grinding purposes.

Man is an omnivorous feeder; this habit has enabled him to accommodate himself to a varied subsistence of flesh, fowl,

fish, grain or fruit, and to persist under conditions which would have been fatal to other creatures.

Closure.—In modern European man the six front upper teeth close over the lower incisors and canines; in older races, as seen in the skulls of the Bronze Age, Romano-British,

Fig. 21.—Occlusion of permanent teeth.

and even mediæval man, the anterior teeth bit edge to edge, as in many lower races of mankind in the present day.

Occlusion.—In occlusion each crown antagonizes with a portion of two opposing crowns, with the exception of the lower central incisors and the third molars.

The central upper incisor, being much broader, closes over the lower central incisor and half of the lateral; while the upper lateral incisor closes over half of the lower lateral and half of the canine, the sweep of the upper anterior teeth being wider than those in the mandible.

The upper canine closes over the posterior half of the lower canine and the anterior portion of the first lower bicuspid.

The first upper premolar shuts between the first and second lower premolar.

The second upper premolar impinges upon the distal portion of the crown of the second lower premolar and a third of the crown of the first lower molar.

The upper first molar covers two-thirds of the lower first molar and part of the lower second molar.

The upper second molar closes on the posterior portion of crown of lower second molar and the anterior part of the lower third molar.

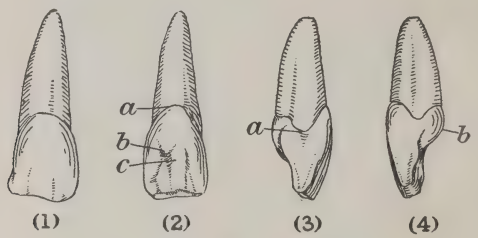


Fig. 22.—Central upper incisor.
a, cervical line; *b*, cervico-lingual ridge; *c*, lingual fossa.
Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

The upper third molar, by reason of its small size, occludes with the opposing lower third tooth.

The external cusps of the lower teeth close in the spaces between the external and internal cusps of the upper crowns.

Each tooth is composed of crown, neck and root. The crown is the portion visible above the gum, and is embedded in the alveolus by one or more roots: while the neck is the junction of the crown and the root.

Surfaces.—A crown has usually five surfaces—

1. *Labial*, applied to the external surface of the anterior teeth; behind the canines the term *buccal* is used.
2. *Lingual*, the internal aspect.
3. *Mesial*, the surface directed to the median line of the jaw.
4. *Distal*, the posterior side.
5. *Occlusal*, the masticating surface of the tooth.

The Maxillary Teeth

The incisors are somewhat flattened, chisel-shaped teeth, with cutting edges for biting food.

Central Incisor.—The crown of the central incisor is wide, though longer than broad, tapering towards the apex, suggesting a triangular appearance, the cervical margin being the apex; viewed sideways it appears wedge shaped. When first erupted three small cusps occupy the biting edge, but disappear early.

The mesial angle is acute, the distal rounded.

A

B

Fig. 23.—Human dentition.
A, Teeth of left side of upper jaw. B, Teeth of left side of lower jaw.

The labial aspect is convex, the lingual concave, and the basal ridge, or cingulum, is raised, sometimes forming a lingual cusp. Immediately above it is the lingual fossa. On the mesial and distal surfaces the enamel border or cervical line is produced into a V shape, the apex pointing upwards to the cutting edge. At the neck there is little constriction, the enamel margin following the irregular contour of the crown.

The root is single, straight, stout, and somewhat conical, the labial surface widest.

The pulp cavity follows the contour of the crown, rising into three cornua, the central disappearing early. A section of the tooth mesio-distally shows the pulp cavity as a double cone, one apex terminating in the crown, the other in the root, the widest portion being at the cervical margin. In a transverse section of the root the cavity is circular.

The **Lateral Incisor** is similar in shape, but much smaller, the distal edge more rounded, and the narrowing of the crown to the base more pronounced.

The lingual aspect is more concave and the basal cingulum is frequently raised to form a cusp, which is more apparent than in the central incisor.

The root is slightly compressed from side to side, with the same arrangement of the enamel border, dipping into the V-shaped spaces, mesially and distally. The pulp chamber resembles that of the central incisor but is larger in proportion to the size of the tooth.

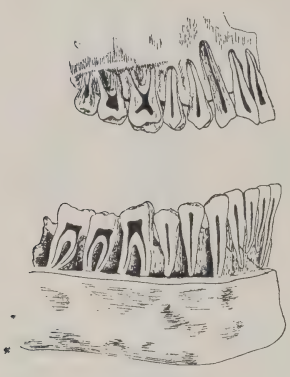


Fig. 24.—Pulp chambers in human teeth.

The **Canine** is a strong conical tooth, with thick pointed crown, deeply implanted by a long root, which is rounded and laterally compressed, the raised socket bone forming the canine eminence, which gives character to the face.

It is no longer a weapon of offence, and being now on the same level as the other teeth its character is unsuspected.

The surface of the crown is unequal, rapidly sloping from the apex of the cusp on either side, mesially and distally, the slope on the distal side being the greater.

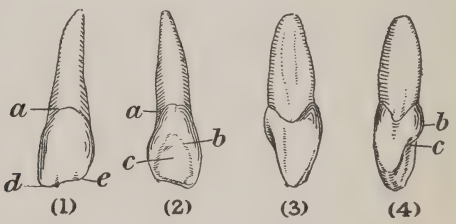


Fig. 25.—Lateral incisor (upper) left.

a, cervical line; *b*, cervico-lingual ridge; *c*, lingual fossa; *d*, mesial angle; *e*, distal angle.

Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

On the labial face the crown is convex, with a rounded border on the gingival margin; on the lingual face a strong ridge of enamel extends from the enlarged and thickened cingulum to the blunt point on the apex of the crown, with a groove on either side, the lingual grooves.

The mesial area is slightly convex, while the distal area is larger and flatter.

The crown is somewhat triangular in section, the neck is less distinct as the root merges into the crown, with but slight

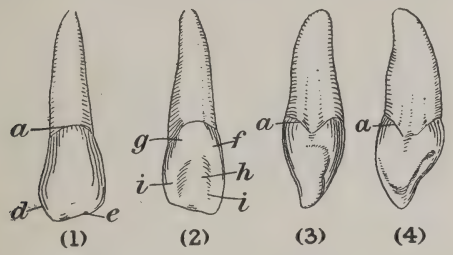


FIG. 26.—Upper canine (left).

a, cervical line; *d*, mesial angle; *e*, distal angle; *f*, mesio-marginal ridge; *g*, disto-marginal ridge; *h*, lingual ridge; *i*, lingual groove.

Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

constriction, the V-shaped contour of the enamel border, mesially and distally, is present.

The pulp chamber is very large, following in shape the contour of the tooth, without cornua, being widest in the centre, tapering at each end, shaped like a double cone (fig. 27).

FIG. 27—Longitudinal section of canine.

First Premolar.—The first bicuspid or premolar is, as its name implies, two cuspid, the buccal cusp, formed by the union of four ridges, being longest and largest, and somewhat pointed, the lingual cusp is rounder, more bulbous, narrowing rapidly at the base.

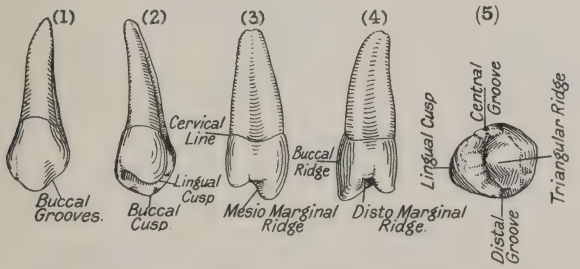


FIG. 28.—First upper premolar (left).

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

A deep groove (median) separates the two cusps on the occlusal surface, extending slightly over the mesial border,

but stopping short of the distal, where the margin is raised and most pronounced.

The neck is horizontal, dipping slightly mesially and distally, the mesial surface is somewhat concave.

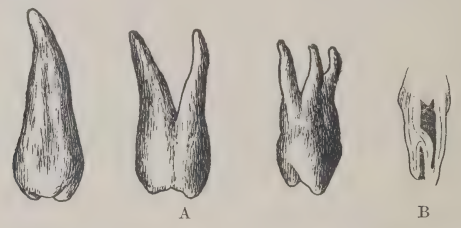


FIG. 29.—First upper premolar. *A*, roots; *B*, longitudinal section.

The root is variable, usually single, and grooved longitudinally on the mesial and distal surfaces, occasionally it is bifurcated, or even two rooted, and in some instances three roots are present, as in the anthropoid apes.

The pulp chamber is large, somewhat square, following in the roots the shape of the divisions (fig. 29).

Second Premolar.—The second premolar is similar in shape to the first, but larger, both cusps being raised to the same level, giving a molariform appearance to the crown, which is further pronounced by the raising of the cingulum, mesially and distally.

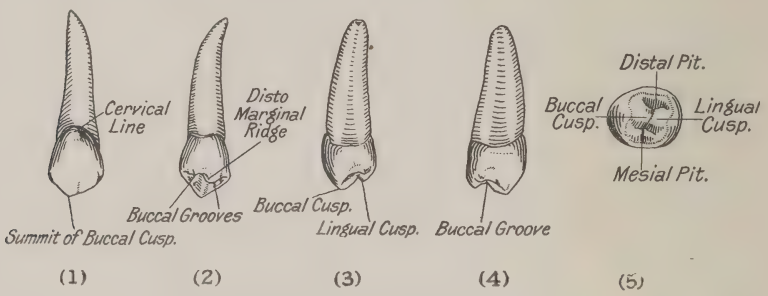


FIG. 30.—Second upper premolar (left).

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

The transverse groove on the occlusal surface is less deep and does not cross the mesial border, and the buccal cusp is more rounded.

The mesial and distal surfaces are flattened, the concavity on the mesial side is absent, the root is single and not given to variation, flattened and grooved mesially and distally.

The pulp chamber is large, oblong in shape, developing into cornua under the cusps.

First Molar.—The first molar is the largest of the series, the second and third molars decrease in size.

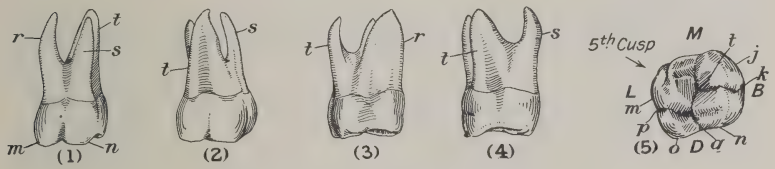


FIG. 31.—First upper molar (left).

j, mesio-buccal cusp; *k*, buccal groove; *l*, central fossa; *m*, mesio-lingual cusp; *n*, disto-buccal cusp; *o*, disto-lingual cusp; *p*, disto-lingual groove; *q*, distal fossa; *r*, mesio-buccal root; *s*, disto-buccal root; *t*, lingual root.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

It consists of a large square crown with rounded angles, quadricuspid, and unevenly divided by an oblique ridge of enamel, which unites the large antero internal or mesio-lingual with the posterior external cusp or disto-buccal.

The molar suggests an evolution from a tricuspid crown by the raising of the cingulum on the distal surface to form a fourth cusp, so that man's first upper molar probably retains impressed upon its crown the record of its development from a tritubercular origin.

Occasionally the first molar has an additional cusp, usually on the lingual face, rendering the crown quinque-cuspid, and this is often seen on the second upper temporary molar also.

FIG. 32.—Left upper first molar.

FIG. 33.—Supplemental lingual cusp in upper molar.

FIG. 34.—Supplemental lingual cusp in milk upper molar.

Two *grooves* traverse the occlusal surface of the crown; the anterior or buccal, starting from the buccal surface, separates the two external cusps and ends in the concavity or central fossa on the occlusal surface.

The posterior groove runs obliquely at the back of the

oblique ridge, from the disto-buccal cusp, across the crown, and over the lingual surface, where it terminates.

The first molar is implanted by three large divergent roots, two buccal, which are flattened mesio-distally, the first being the larger, and one curved, conical, lingual root, which is the biggest of the three.

The neck of the tooth is much constricted, giving a bell-shaped appearance to the crown, with its horizontal border line of enamel, which it appears to overhang. The pulp chamber is dumb-bell shaped in section; in the lingual root it is large and circular, tapering to the apex, while in the buccal roots the pulps are somewhat flattened, following their contours.

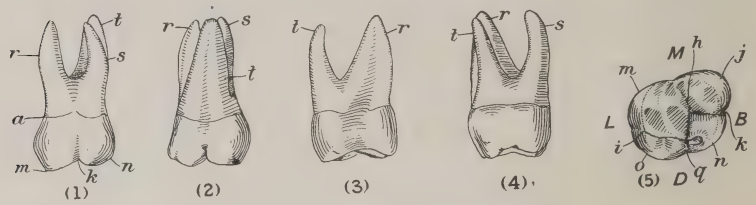


FIG. 35.—Second upper molar (left).

a, cervical line; *k*, buccal groove; *m*, mesio-buccal cusp; *n*, disto-buccal cusp; *i*, lingual groove; *l*, central fossa; *o*, disto-lingual cusp; *r*, mesio-buccal root; *s*, disto-buccal root; *t*, lingual root.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

Second Molar.—The second molar is smaller, the occlusal surface of the crown has the same characteristics as in the first molar, though frequently the lingual cusps are somewhat fused, giving a tritubercular appearance. The crown is more compressed and less square, the disto-lingual cusp being feebly developed, the roots are smaller, and often fused.

The pulp chamber resembles that in the first molar, but is more constricted and has less of the dumb-bell contour of the former.

Third Molar.—The third molar is very changeable in form, varying from a tooth with crown and roots of the same pattern as in the first molar to a degraded stunted cone, with a single root.

In many instances, in consequence of the reduction in size of the jaws brought about by civilization, the third molar is suppressed altogether, in others it is retained in its crypt and never erupts.

The Mandibular Teeth

The four lower incisors are arranged vertically and in a straight line in the front of the mandible.

They are narrower in their crowns than are the upper incisors, square edged on the biting surfaces, when first erupted each crown is surmounted by three small cusps on the incisive edge.

Central Incisor.—The central incisor is smaller than the lateral, the crown is wedge shaped, somewhat triangular, becoming rapidly attenuated towards the gum margin, the root is much compressed, thin and grooved mesio-distally,

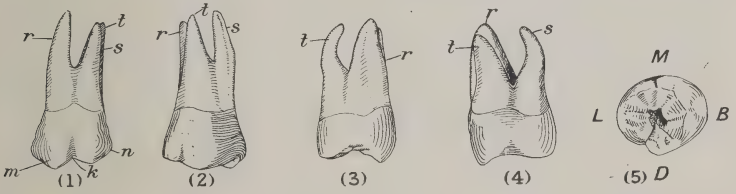


FIG. 36.—Third upper molar (left). Cusps of crown coalesced.

k, buccal groove; *m*, mesio-buccal cusp; *n*, disto-buccal cusp; *r*, mesio-distal root; *s*, disto-buccal root; *t*, lingual root.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

the crown and root run together with little break at the neck, the cingulum is not raised.

The convex labial surface of the crown is broader than the lingual, the latter being concave, thinning to a blade on the biting edge, while the mesial and distal aspects are flattened.

The horizontal border is slightly elevated, mesially and distally, having the triangular disposition of the enamel margin as in the upper incisor.

The pulp chamber is very narrow, constricted and hairlike.

Lateral Incisor.—This tooth is similar to the central, but larger, with a longer root and wider crown.

The labial surface of the crown is flatter and the lingual less concave.

The cervical line is continued into the triangular spaces, mesially and distally, the root is thicker, and rounder at the cervical margin, but flatter laterally; the pulp chamber is hairlike.

Canine.—The canine is smaller and narrower than the

upper tooth, with a longer crown, surmounted at first by a blunt point.

The labial surface is convex in both directions; on the lingual face a ridge of enamel unites the basal cingulum with the blunt point at the apex of the crown.

Fig. 37.—Bifurcated root of lower canine.

The crown is thick at the base, having a greater slope distally, where the aspect is convex, while the mesial side is flattened.

The root is narrower, its surfaces more compressed, with longitudinal grooves, mesially and distally, and occasionally bifurcation occurs (fig. 37).

The pulp cavity is narrower and more conical than in the upper canine.

First Premolar.—The first lower premolar has a small crown, rounded, somewhat bent inwards, like the first lower premolar of the anthropoid apes. The buccal surface is convex, contracting at the cervical margin, produced on the summit into a blunt

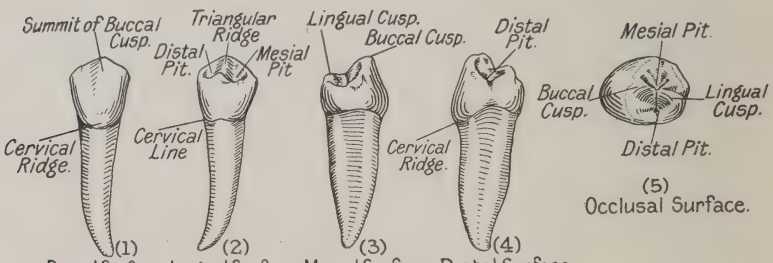


Fig. 38.—First lower premolar (left).

point; on the occlusal face the cingulum is elevated into a low lingual cusp, united by a ridge with the buccal cusp; on either side of the ridge is a mesial and distal pit, and the marginal ridge is also raised mesially and distally.

The cervical margin is thickened with a rounded border, the distal surface being slightly triangular; the root is flattened and grooved on the mesial and distal surfaces, the pulp chamber thin and bristle-like; one small point penetrates the lingual cusp.

The **Second Premolar** is larger than the first, the crown broader and molariform, and the root more round.

The occlusal surface is somewhat square, the lingual cusp being raised to the same level as the buccal, while the cingulum is elevated mesially and distally. It is traversed by a fissure, ending in a mesial and distal pit, and a narrow groove

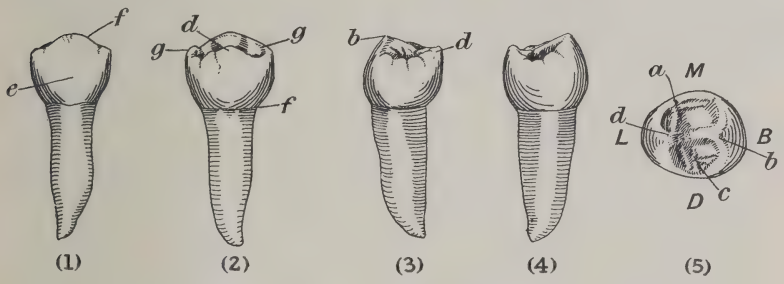


FIG. 39.—Second lower premolar (left).

a, mesial pit; *b*, buccal cusp; *c*, distal pit; *d*, lingual cusp; *e*, buccal ridge; *f*, cervical line; *g*, marginal ridge.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Distal. 4. Mesial. 5. Occlusal.

crosses the occlusal surface, mesially and distally, giving a quadricuspid appearance.

The buccal surface is convex in each direction, often a small buccal groove is present anteriorly, crossing the cutting edge. The face of the crown is not equal, the distal edge being the longest.

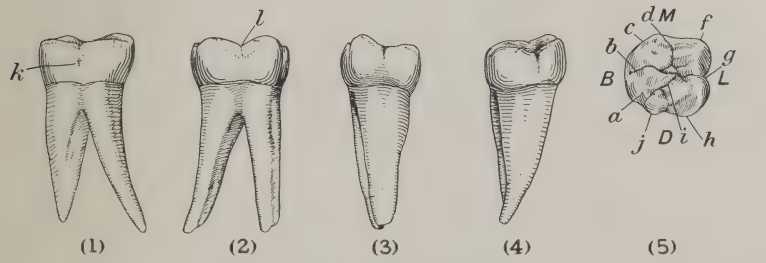


FIG. 40.—First lower molar (left).

a, buccal cusp; *b*, buccal groove; *c*, mesio-buccal cusp; *d*, mesial groove; *e*, central fossa; , mesio-lingual cusp; *g*, lingual groove; *h*, disto-lingual cusp; *i*, distal groove; *j*, disto-buccal cusp; *k*, buccal pit; *l*, lingual groove.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

The lingual surface is convex, the elevated ring of the cingulum carrying the pointed lingual cusp upwards.

The mesial surface is convex and slightly flattened at the

neck; this description equally applies to the distal surface, where, however, the convexity is more pronounced.

The root is stout and less tapering than in the first premolar, and flattened and often grooved, mesially and distally.

The neck is less constricted by reason of the gradual convergence of the crown to the root, the enamel border encircling the tooth in a ring-like fashion, without deflection.

The pulp cavity follows the contour of the crown, the cornua being small; the cavity narrows without a break, tapering towards the extremity of the root.

First Molar.—The first lower molar is the largest of the series, with a rectangular quinque-cuspid crown implanted by two roots.

The crown is shorter in proportion than the first upper molar and less deep, longer than broad, having on the occlusal

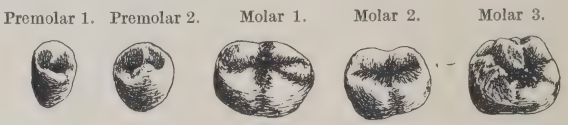


Fig. 41.—Crowns of human lower cheek teeth (right).

surface five rounded cusps, two buccal, two lingual and one disto-buccal.

The occlusal surface is divided by a crucial fissure, separating the buccal and lingual cusps; the posterior or distal arm bifurcates and encloses the disto-buccal cusp.

The grooves traversing the occlusal surface are the buccal, lingual, mesial, distal and disto-buccal; the buccal and lingual grooves cross over the surface of the crown, the buccal terminating in the buccal pit.

The cusps are buccal, lingual, mesial, distal and disto-buccal, the last is the smallest; its presence makes the crown unequal, so that mesially it is squarish, with acute angles, while distally it is rounded.

The mesio-buccal cusp is the largest, and is double the size of the buccal cusp; both lingual cusps are somewhat pointed.

A marginal ridge unites the various cusps, and is especially evident on the mesial and distal surfaces.

The buccal surface of the crown is convex in both directions,

showing the small pit near the occlusal margin where the buccal groove terminates, and is wider than the lingual surface.

The lingual surface is likewise convex in each direction, with a notch on the summit, where the lingual groove crosses over, and is sometimes prolonged as a shallow furrow, dividing the lingual surface.

The mesial surface is flattened but slightly rounded at the point of contact with the crown of the second bicuspid, the margin at the base being somewhat concave.

The distal surface is convex by reason of the presence of the disto-buccal cusp. The buccal cusps are worn away before the lingual.

FIG. 42.—Longitudinal section of first lower molar.

The tooth is implanted by two strong roots, mesial and distal, both wide apart and slightly curved backwards; each is flattened and grooved on the mesial and distal surfaces. The mesial root is the largest and the most curved. The pulp chamber is large, following the contour of the crown, being sometimes square and in others constricted or hour-glass shaped in the middle, the canal in the mesial root being the largest; both pulp chambers are flattened and the cornua prolonged beneath the cusps.

Second Molar.—This tooth is smaller than the first molar,

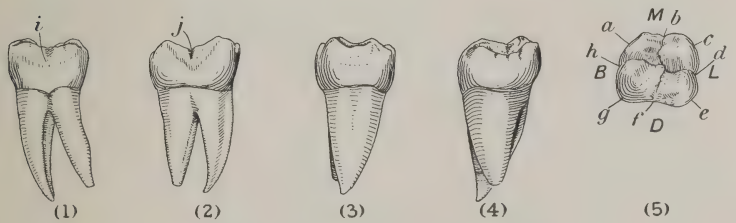


FIG. 43.—Second lower molar (left).

a, mesio-buccal cusp; *b*, mesial groove; *c*, mesio-lingual cusp; *d*, lingual groove; *e*, disto-lingual cusp; *f*, distal groove; *g*, disto-buccal cusp; *h*, buccal groove; *i*, buccal pit; *j*, lingual groove.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

and in European races usually quadricuspid, the cusps being equal in size, so that the crown is symmetrical by reason of the absence of the disto-buccal cusp.

The occlusal surface is divided by a crucial fissure which traverses the crown, the buccal arm, as in the first molar, crossing over the buccal surface and terminating in the buccal pit, while the lingual groove passes over the lingual aspect, dividing it into two halves.

Except for the absence of the fifth cusp the second molar resembles the first, but the roots are smaller, often more or less united, converging at the apices.

In the Zulu race the second lower molar is quinque-cuspid, like the first molar, and the same characteristic is seen in some Europeans.

The pulp chamber resembles that of the first molar, but the characteristics are less pronounced.

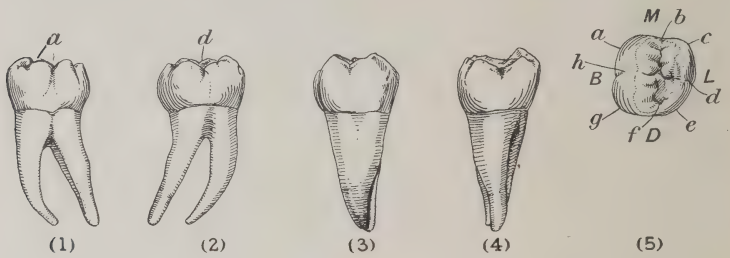


FIG. 44.—Lower third molar (left).

a, mesio-buccal cusp; *b*, mesial groove; *c*, mesio-lingual cusp; *d*, lingual groove; *e*, disto-lingual cusp; *f*, distal groove; *g*, disto-buccal cusp; *h*, buccal groove.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

Third Lower.—This tooth varies considerably in shape, sometimes being quinque-cuspid, as in the first lower molar, in which case the fifth cusp is external and in line with the buccal cusps, or it may have four cusps, as in the second molar.

In other cases the cusps are so distorted as to be difficult to recognize.

The same description applies to the roots, which normally are two rooted, but are extremely variable, and often completely united; a condition produced by the contraction of the jaws in the higher races, limiting the space for the accommodation of the wisdom teeth. For this reason the third molars are often unerupted and remain concealed in the alveoli. In primitive races, where the jaws are massive and well developed, the roots are all separate.

In the Australian black the third molars are as large as the first, and in the early Palæolithic man of Spy the molars

actually increase in size, from the first to the third, the roots being all distinct.

In all three molars the pulps resemble one another.

Deciduous Dentition

Number.—The deciduous or milk teeth are twenty in number, represented by d.i. $\frac{2}{2}$, d.c. $\frac{1}{1}$, d.m. $\frac{2}{2}$.

General Characteristics.—The teeth are smaller than those of the permanent series, but they partake largely of the patterns of their successors, with the exception of the first milk molars.

On the whole the crowns are shorter, more bulbous, the cervical margins more abrupt, the necks much constricted, since the crowns are wider than the roots at their junction and the pulp chamber much larger.

Fig. 45.—Occlusion of Temporary Dentition.

The Maxillary Teeth

Central Incisor.—The central incisor resembles its permanent successor; the crown is short, broader than it is long, the incisive edge is square mesially, but rounded distally.

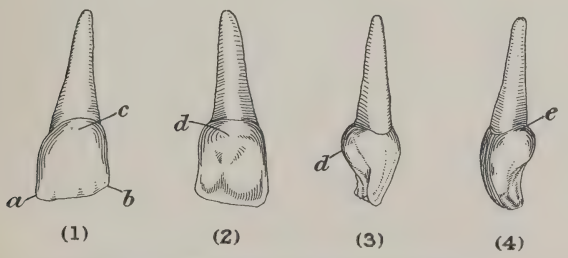


Fig. 46.—Left upper central incisor (milk).

a, mesial angle; *b*, distal angle; *c*, cervical ridge; *d*, cervico-labial ridge; *e*, cervical line.

Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

The labial surface of the crown is convex; the lingual surface is concave, becoming flattened at the biting edge; the basal ridge is thickened and raised.

The mesial and distal surfaces are rounded and lack the triangular spaces which are seen in the permanent incisors, the marginal ring of enamel running horizontally around the crown.

The root is longer in proportion to the crown than in the permanent tooth; it is circular, with the pulp canal large and rounded.

Lateral Incisor.—This tooth is much smaller, the cutting edges of the crown are considerably rounded, especially the distal angle. The crown narrows rapidly towards the neck,

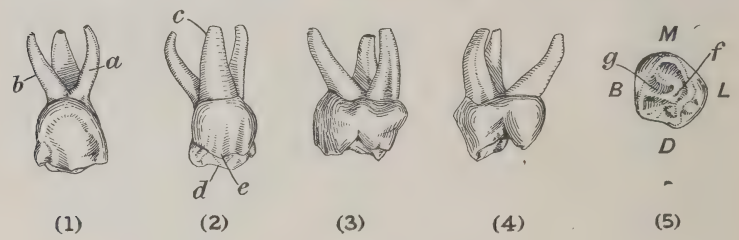


FIG. 47.—First upper milk molar (left).

a, mesio-buccal root; *b*, disto-buccal root; *c*, lingual root; *d*, buccal cusp; *e*, lingual cusp; *f*, central furrow; *g*, buccal ridge.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

having a somewhat caniniform appearance, and the cingulum is pronounced. The root is oval, compressed slightly mesially and distally, and the pulp chamber is circular.

Canine.—The crown is bulbous, stout and pointed, the marginal slopes running downwards from the point, mesially and distally, are almost equal, giving the tooth an ape-like appearance, and the apex projects above the other teeth. The labial surface is broad and convex in each direction, the cervical margin being very abrupt. On the lingual surface the basal ridge is thickened and a longitudinal ridge unites the base with the pointed cusp on the summit.

The root is long and circular, the large pulp chamber following its contour.

First Molar.—The first molar has an occlusal surface surmounted by three cusps, two of which are placed upon its buccal, and one on its palatal surface. The buccal surface

is very convex, more especially over the anterior buccal root, where the enamel is rounded and thickened; the lingual surface, convex in each direction, has a globular appearance by reason of the extreme contraction at the neck.

A deep furrow crosses the occlusal surface separating the buccal and lingual cusps, and passes over the mesial border.

The roots are three, two buccal and one lingual, the former flattened mesio-distally, the latter being the largest; all are divergent to accommodate the crown of the first premolar.

Second Molar.—The second molar closely resembles the first permanent molar.

The occlusal surface possesses the same characteristics, but

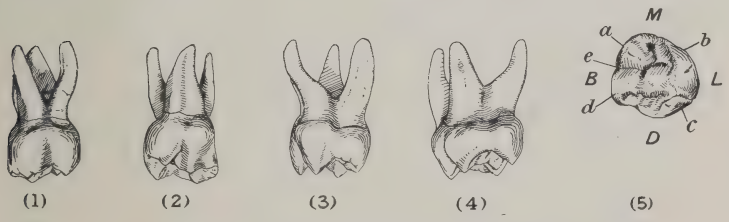


FIG. 48.—Second upper milk molar (right).

a, mesio-buccal cusp; *b*, mesio-lingual cusp; *c*, disto-lingual cusp; *d*, disto-buccal cusp; *e*, buccal groove.

Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

the cusps are more pointed, the grooves deeper, and the transverse ridge better defined.

The disto-lingual cusp is less raised and the distal groove is more evident.

The three roots resemble those of the first permanent molar, but are much more divergent to accommodate the crown of the second premolar.

The Mandibular Teeth

The **Incisors** closely resemble the permanent teeth, therefore it is not necessary to describe them in detail.

Canine.—The grooves and markings are less distinct than in the permanent lower canine, the crown is shorter in proportion and much more bulbous.

First Molar.—The first molar has a short, squat, oblong crown, compressed from the lingual to the buccal side.

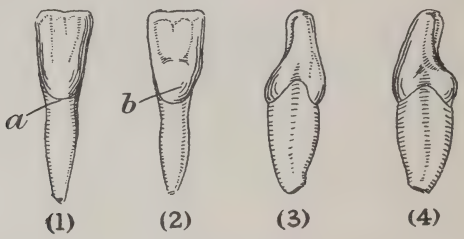


Fig. 49.—Central milk lower incisor.
a, cervical line; *b*, cervico-labial ridge.
Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

The buccal surface is flattened, but an enlarged convexity exists near the neck above the anterior buccal root, giving a

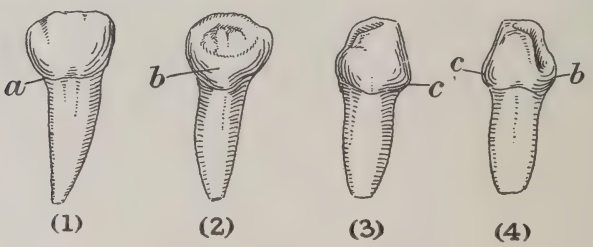


Fig. 50.—Lower milk canine.
a, cervical line; *b*, cervico-labial ridge; *c*, labial ridge.
Tooth Surfaces.—1. Labial. 2. Lingual. 3. Mesial. 4. Distal.

bulbous appearance; at this point also the crown is much deeper, becoming more shallow towards the distal end, the

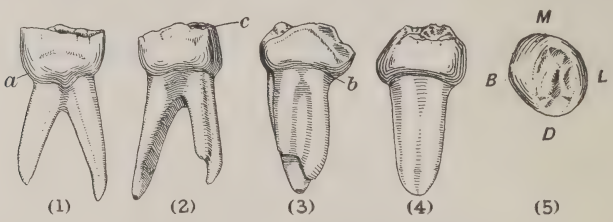


Fig. 51.—Lower first milk molar (left).
a, mesio-buccal convexity; *b*, constricted neck; *c*, marginal ridge.
Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

neck likewise is much smaller than the crown and very constricted.

The lingual surface is convex in all directions and is surmounted with two unequal sharp-pointed cusps, the anterior being the larger.

A low ridge crosses the occlusal surface uniting the anterior buccal and the mesio-lingual cusps. Two grooves, mesial and distal, traverse the crown, one in front of the mesial ridge, the other behind, both emerging on the lingual surface by deep notches on the marginal crest, thus isolating the large pointed anterior internal cusp.

A central groove runs the length of the occlusal surface, crossing over the mesial and distal borders, where the cingulum

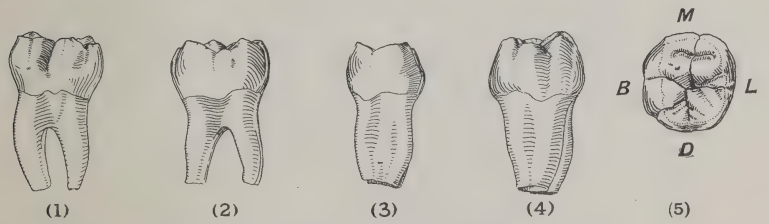


Fig. 52.—Second lower milk molar (left) at 4 years.
Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

is elevated considerably as a marginal ridge. There are two roots, flattened mesio-distally, and widely divergent.

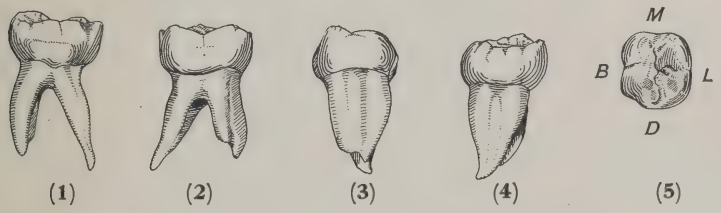


Fig. 53.—Second lower milk molar (left) at 5 years.
Tooth Surfaces.—1. Buccal. 2. Lingual. 3. Mesial. 4. Distal. 5. Occlusal.

Second Molar.—The second lower molar resembles the first permanent lower molar, only the disto-buccal cusp is more external, being in line with the other buccal cusps ; the crown is more constricted at the neck and the two roots, flattened mesio-distally, diverge to embrace the developing premolar crown, otherwise the grooves, pits and

marks on the occlusal surface are identical with the permanent molar.

Human Dental Abnormalities

Supernumerary Incisors.—Occasionally in the intermaxillary bone are seen one and sometimes two teeth, usually

Fig. 54.—Right and left upper permanent supplemental incisors.

of a conical form, which perhaps may be regarded as a reproduction of the missing incisors; when present they distort the permanent teeth considerably, crowding them out in all directions and disfiguring the mouth; they are usually situated behind the central incisors or in the median line between them, and occasionally the crown tends to be molariform.

Supplemental Incisors.—More rarely it happens that an additional incisor is present, so like the other teeth that its character would hardly be suspected, especially when, as in some instances, the supplemental tooth is in series with the others and the symmetry is not disturbed.

Generally, however, it erupts in the palate, and sometimes both the missing teeth appear, leading to overcrowding and distortion. This characteristic is not confined to the per-

Fig. 55.—Deciduous supplemental right upper incisor.

manent set, for observation will show that supplemental incisors, either singly or in a pair, are not uncommon even in the milk dentition, and are subsequently followed by

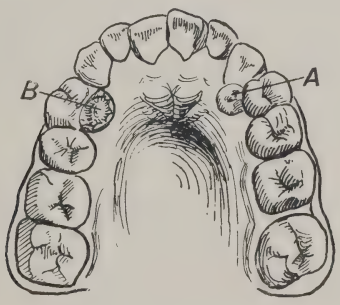


Fig. 56.—Upper teeth with a third pair of premolars at A and B.

permanent supplemental teeth ; might not this be considered as a reversion to the primitive ancestor of the primates in the Eocene, with its archetypal dental formula of i. $\frac{3}{3}$?

It is unusual to find supplemental incisors in the mandible, but now and then it occurs ; in one rare instance only have I found the lower six incisors in place. Supplemental canines are unusual. Additional premolars are extremely rare.

The existing premolars are considered to be the third and fourth premolars of the permanent mammalian dentition. A fourth molar, sometimes of normal size, but more frequently stunted and functionless, appears in the upper jaw, either on the buccal side or at the extremity of the series, and is by no means uncommon in some of the lower races.

The Temporo-Mandibular Articulation

Anatomy of the Bone Surfaces.—An examination of the mandibular (glenoid) fossa at the base of the skull shows it to be divided into an anterior and posterior portion dissimilar in character and separated from one another by the petro-tympanic fissure. The bony wall of the posterior portion is formed by the tympanic part of the temporal bone which intervenes between the mandibular fossa and the external auditory meatus : its surface is rough and it is occupied by a portion of the parotid gland. The surface of the anterior portion is smooth, and it this portion which enters into articulation with the mandible. It is concave downwards, and posteriorly it ends abruptly at the petro-tympanic fissure ; a small process of bone growing downwards from the posterior root of the zygoma—the post-glenoid process—also marks its posterior limit laterally. This process attains a much greater development in the anthropoid apes, and a greater still in carnivora, where it plays an important part in preventing posterior movement of the mandibular condyle. Anteriorly the concavity of the mandibular fossa passes into the convexity of the articular tubercle (eminentia articularis), a smooth elevation on the lower surface of the squamous portion of the temporal bone which is continuous with the anterior root of the zygoma. The surface both of the anterior portion of the mandibular fossa and of the articular tubercle are encrusted with hyaline cartilage and clothed with synovial membrane in the fresh state, and both surfaces therefore enter into the formation of the joint. The articular tubercle is very slightly developed in infancy : it then resembles its condition in the apes, in which it is represented only by a flat articular plane.

The condyle of the mandible is a cylinder with its long axis directed from without inwards and backwards, its upper

surface being clothed with hyaline cartilage and synovial membrane. It is separated from the articular surface of the temporal bone by a disc of fibro-cartilage which divides the joint into an upper and lower compartment each lined with its own separate synovial sheath. The upper of these is the larger and looser of the two, extending as it does forward on to the articular tubercle, and permits therefore a greater range of movement than the lower.

The inter-articular cartilage is a thin, oval disc whose upper and lower surfaces conform to the very dissimilar bony surfaces which it separates. Thus, its upper surface is concavo-convex from before backwards and its lower surface is concave. Its edge is attached to the capsule of the joint, and in front provides insertion for some tendinous fibres of the external pterygoid muscle. Thus, in protraction of the mandible, it accompanies the condyle in its movement forwards. The function, therefore, of the cartilage is to facilitate those gliding movements, particularly the movement of rotation, which would be hampered if the condyle fitted into the deep mandibular fossa. It also serves to reduce wear and tear of the joint.

The Ligaments.—The temporo-mandibular joint derives its strength mainly from the very powerful muscles that support the mandible and only to a small degree from its ligaments. The capsular ligament which envelops both compartments of the joint, though complete, is thin and loose in texture and permits a wide range of movement. There are, however, certain accessory ligaments arranged to check movement in undesirable directions.

The temporo-mandibular ligament (external lateral ligament) is attached above to the zygomatic process of the temporal bone and below to the lateral and posterior aspects of the neck of the mandibular condyle. It is arranged in two bands directed obliquely downwards and backwards, so that it prevents backward displacement of the condyle while permitting the forward movement of protraction. It also checks excessive depression of the mandible.

The spheno-mandibular ligament is situated on the medial or internal aspects of the joint. It is attached above to the angular spine of the sphenoid bone, whence it runs forwards and downwards to become attached around the margin of the

inferior alveolar foramen. It is therefore separated from the joint by a space in which lie parts of the internal maxillary, inferior alveolar and middle meningeal vessels, the inferior alveolar and auriculo-temporal nerves, and the external pterygoid muscle. Its presence tends to immobilize the middle

Fig. 57.—Temporo-Mandibular Articulation (internal view).

portion of the ascending ramus of the mandible during movements of the joint and so prevent undue stretching of the inferior alveolar vessels and nerve as they enter the bone.

The stylo-mandibular ligament is a specialized portion of the deep cervical fascia which extends from the tip of the styloid process to the posterior border of the angle of the mandible: its effect on joint movement is unimportant.

Movements at the Joint.—These are complicated by the fact that the temporo-mandibular articulations on either side

may act simultaneously but in a dissimilar manner. On analysis, however, it will be found that the great variety of movements permitted, resolve themselves into two primary ones, their converse and their combinations.

Gliding Movement. (*a*) In *protraction* the condyle, accompanied by the inter-articular fibro-cartilage glides forward and mounts the articular tubercle, thereby causing simultaneously with the forward movement a depression of the angle of the mandible and separation of the molar teeth. The movement takes place entirely in the upper compartment of the joint, and though usually associated with a hinge movement in the lower compartment resulting in opening of the mouth, is not necessarily accompanied by the latter, as the incisors can be kept continuously in contact during protrusion.

The disturbance to the effective occlusion of the molars, which would otherwise result from the depression of the angle of the mandible, is prevented by an arrangement of their occlusal surfaces in a curve with its convexity downwards (curve of Spee). In infants, in the anthropoid apes, and still more in the ungulates, the articular tubercle is deficient, protrusion is not necessarily accompanied by depression, and the curve of Spee is very slight or absent.

(*b*) *Retraction* is the reversal of the movements previously considered and needs no further description.

(*c*) *Rotation*, or lateral gliding movement, results from alternate unilateral protraction and retraction. The resulting movement is approximately one of rotation of the mandible round a vertical axis running through the centre of the retracted condyle. It is, however, complicated by the depression of the angle of the mandible on the side on which protraction takes place, resulting in tilting of this vertical axis from side to side. The occlusion of the molars compensates for this tilting by a transverse occlusal curve with its convexity downwards, the upper molars presenting slightly outwards, the lower molars slightly inwards. Rotation is facilitated by the oblique direction of the mandibular condyle. In infants and in the anthropoid apes little rotary movement is employed, the axis of the condyle is almost transverse, and the transverse occlusal curve of the molar teeth is not developed.

Hinge Movements. (*a*) In *depression* of the mandible the condyle rotates round a horizontal axis on the under surface

of the inter-articular cartilage, so that the movement takes place entirely in the lower compartment of the joint. Such a movement cannot, however, be produced alone, but is invariably associated with protrusion of the condyles and the accompanying depression of the angle of the mandible. In practice, therefore, the path described by the mandible when the mouth is opened is not the arc of any one circle, but segments of a series of similar circles each described from a more advanced centre. The movement is complicated not only by the associated protrusion, but by the attachment of the spheno-mandibular ligament (see Fig. 57). The result is a movement which approximates to the flattened arc of a circle round a transverse horizontal axis running through the ascending ramus of the mandible a little behind the inferior alveolar foramen.

(*b*) *Elevation* of the mandible or closure of the mouth is the reversal of the movements previously described, and is, of course, accompanied by retraction of the mandible.

The Muscles of Mastication.—For detailed description of the muscles of mastication and their attachments, the student is referred to text-books of Anatomy. A short discussion of their functions is, however, necessary to complete a description of the temporo-mandibular joint. It should first be emphasized that they form a single balanced group, no one member of which acts alone, but is invariably controlled by tonic action of the others. In addition to producing movement they form the principal factor in the strength of the joint, the mandible being slung from its angle against the base of the skull.

The masseter muscle produces powerful occlusion of the incisor and canine teeth when the mandible is protracted, i.e. it is the muscle of "biting" as opposed to "grinding." It plays only a slight part in the rotary movements associated with mastication between the molar teeth. It is therefore well developed in carnivora, where the incisors and canines are strong and the action of "biting" is the chief function of the jaws.

The temporal muscle is the chief agent in closure of the mouth. Its posterior fibres running horizontally, draw the condyle backwards, while its anterior fibres produce the hinge movement necessary for elevation of the mandible. It there-

fore opposes the external pterygoid muscle, and the two together are the principal muscles involved in rotation of the mandible and the movements of the molar mastication.

The external pterygoid muscle produces protraction of the mandible. Working in conjunction with the temporal muscle of the opposite side and alternately with its fellow, it produces rotary movements of the mandible. It is therefore strongly developed in herbivora, in whom these movements are prominent. By pulling the condyle forwards it also plays the chief part in the movement of depression of the mandible. In both these movements it is partially assisted by the internal pterygoid muscle.

The internal pterygoid muscle is supplementary to the masseter and external pterygoid muscles respectively, assisting both incisor and canine occlusion and the movement of protraction.

The muscles attached to the hyoid bone below and the mandible above, i.e. the digastric, genio-hyoid, and mylo-hyoid, play a minor part in the depression of the mandible, being assisted by gravity in producing that movement. Their chief function however is by their contraction to keep the hyoid bone elevated when the mandible is depressed. They can only act on the mandible when the hyoid bone is fixed by contraction of the infra-hyoid group of muscles, but the part they play is probably inferior to that of the external pterygoid.

CHAPTER III

THE PROCESS OF THE ERUPTION OF THE TEETH

Theories to Explain the Eruption of the Teeth

Various theories have been suggested to explain the eruption of the teeth, and these will be stated briefly.

Blood Pressure.—Immediately before and during the eruption of the teeth there is an increased flow of blood to the adjacent tissues, the pressure from which is considered by some authorities to explain the problem of the release of the developing tooth from its bony covering and its elevation into position in the jaws. Tomes, however, points out that "the erupting tooth is not always in the direction of its long axis as in the developing tooth of the crocodile, where it takes an oblique course, by which it travels underneath the old tooth before moving upwards into position."

Rotary Movement.—Underwood suggests that the teeth are carried upwards by a rotary movement of the soft tissues in which they are embedded, as in the shark, where the mucous membrane carries upwards to the summit of the jaw the successive rows of teeth.

Pressure from Elongation of the Roots.—As the tooth moves onwards into its place, it is still incomplete, for the roots, as yet, are unfinished, and it is thought that additions to the free ends tend to force the crown to its proper level. Against this theory, Tomes points out "that the tooth of a crocodile moves upwards, tooth-pulp and all, obviously impelled by something different from mere elongation." Tomes' researches upon the development and succession of reptilian teeth "clearly show that a force quite independent of increase in their length alters the position and erupts successive teeth."

As opposed to this theory, teeth with well-formed roots are frequently unerupted. The third molars are often retained

in their crypts, and the wearing of dentures will sometimes reveal the presence of unerupted canines.

Pressure from Forming Bone of Crypts.—This theory is supported by little evidence.

Warwick James and A. T. Pitts (Proc. Roy. Soc., Med. Odont. Sect., Vol. V, No. 5, pp. 80–101) consider that the point of eruption of the tooth is determined by columns of epithelium which connect the epithelium of the oral surface with that in the tooth follicle, the columns acting as a guide to the advancing tooth. The movement of the tooth, they consider, is partly brought about by the unequal rates of growth of the tissues surrounding the tooth, and in part by the elongation of the root.

The path of eruption is opened out by the weakening of the fibrous capsule walls by the proliferation of epithelium within the tooth follicle, which is connected with the oral epithelium as above mentioned. This epithelium subsequently degenerates, leaving wide spaces in the connective tissue over the tooth. These spaces increase in size, and either by a separation or rarefaction of tissue, the overlying capsule gradually disappears, the tooth erupting at the point first weakened by the degenerating epithelial cells.

Sir Arthur Keith (*Lancet*, April 15, 1911) has suggested that the eruption of the teeth may be governed by the secretions of those ductless glands, such as the thyroid and pituitary, which are known to be concerned with the growth of bone. This theory, however, like the other theories of eruption, remains at present only a hypothesis.

Process of Eruption in Man

The alveolus, the bone so intimately associated with the developing teeth, is largely affected during their eruption. At first it forms the shell-like crypts, in which the early tooth germs are encased, widely open and incomplete at birth, and afterwards up to the sixth month, growing over the summit of the developing crowns, and enclosing them.

Subsequently, a change takes place, rapid absorption of the alveolus is effected, the bone is removed from half the labial surface of the crypts of the anterior teeth, and from above the erupting crowns, which then emerge from the widely-open orifices into place, in pairs.

The next stage is the re-formation of the alveolus around the necks of the teeth, fixing them securely to the jaw. This is followed by the gradual formation of the roots, and simultaneously the sockets are formed around them, the bone being built up around the lengthening roots.

In the fourth year absorption of the roots of the temporary central incisors commences, followed by the laterals, and this process is continued until the appearance of their successors, taking about three years to complete, by which time the roots have practically disappeared, and the crowns fall off.

The Eruption of the Teeth in Fishes, Bactrachians, and Reptiles

Fishes.—In fishes, where the teeth are formed in great numbers on the bones of the mouth and pharynx, they are constantly lost and continually renewed; and as the attachment differs so markedly in different species, the method of replacement varies accordingly.

In the sharks, rays and dogfishes, the teeth are arranged in successive rows, one behind the other. For instance, in the shark each tooth is attached to the cartilaginous jaw by a fibrous membrane, the outer row of teeth stand erect, those behind are usually recumbent, covered, and concealed by a flap of mucous membrane.

The successive rows of teeth rotate from the interior of the mouth, carrying onwards and upwards the dense fibrous membrane with the teeth attached, which ultimately attain the summit of the jaw. When a tooth is lost, another tooth moves forwards, occupying its place from the row behind. Usually each tooth stands exactly behind its predecessor, but in some cases the successive teeth occupy the interspaces.

To renew the constant loss, fresh tooth germs are continually formed from the free end of the tooth band, which is constantly giving off enamel organ buds, ensuring an endless succession of teeth.

In the Teleostei, or bony fishes, the methods of succession vary considerably.

A. In fishes, as the catfish (Fig. 175), where the bones of the mouth and pharynx fairly bristle with the multitude of teeth, unlimited in number, each tooth germ is produced anew, the oral epithelium sending down into the submucous

tissue enamel organs at different points, where the dentine germs will subsequently appear.

B. In the powerful anchylosed teeth of the pike and angler fish, the tooth germs lie at the base of those in position, each excavating in time a cavity in the coarse bone of attachment, and by absorption displacing its predecessor. This method may be noticed in the wrasse and sheep's-head fishes, and in the pharyngeal teeth of the chub.

In the water dog (*Hydrocyon*) (Fig. 178) is seen one of the most marked methods of this form of displacement and eruption. The structure of the jaws is very strong, almost resembling that of a mammal, the few powerful teeth being anchylosed to the summit of the jaw by a special bone of attachment (see Fig. 178). The successional teeth occupy large crypts in the bone, lying immediately underneath their predecessors, pointing backwards, securely concealed and protected from injury.

When a tooth is lost, the opening of the crypt is widened by absorption, allowing the recumbent tooth to rise into a vertical position, ultimately occupying the position of the missing one, and it is secured to the bone by the special bone of attachment.

The wolf fish (*Anarrhichas lupus*) (Fig. 180) is a somewhat similar example : in a dried specimen cavities can be seen at the base of the teeth in position which were occupied by tooth germs, and each would ultimately by absorption of the surrounding bone have excavated a passage, enabling it to rise, and occupy the place of its predecessor.

C. There are a few instances of socketed teeth in fishes ; in the Barracuda pike (*Sphyræna*) tooth germs are developed from the side of the alveolus in the sockets, which by absorption displace their predecessors vertically : in Lepidosteus, the teeth are also partly socketed ; but in the strange rostral teeth of the saw fish (*Pristis*) (Fig. 172) there is no succession, each tooth being of persistent growth.

Batrachians.—In the frog, the edentulous lower jaw closes immediately behind the teeth in the upper jaw, and in consequence the successional tooth germs are found beneath the bases of the existing teeth, which are removed by the absorption of the bone of attachment, their successors rising and occupying their places.

Reptiles.—Crocodilia. The succession of teeth in the modern crocodile closely resembles that of the Ichthyosaurus (see below); the germ lying similarly on the side of the existing tooth, excavates a passage into the interior, and finally displaces it. Examples occur where two and three successional teeth are borne, one surmounting the other by this means, on the last tooth erupted.

Saurians. The succession of teeth in the *Ichthyosaurus*, an extinct marine lizard of the Mesozoic period, was remarkable; the jaws were widely open gutters in which the large conical teeth stood upright, destitute of sockets. The successional tooth germ was in contact with the side of the tooth, at the base, where it first excavated a cavity, and then penetrated into the interior of the pulp chamber, ultimately displacing its predecessor. In the modern lizards, where the teeth are either anchylosed to the summit, or, as in the Monitor lizard (*Varanus*), by a pleurodont attachment to the jaw bone, cavities are seen on the lingual surface, immediately underneath them; these contain successional tooth germs, to replace by absorption those in position.

Ophidia. In snakes, such as the non-venomous pythons, the successive tooth germs lie parallel in a recumbent position close to the jaw bone enclosed in a fold of connective tissue, which position is necessary for their preservation, as if vertical, they would be subject to injury when the snake seized its prey. When the time for eruption arrives, the teeth move upwards, assuming an upright position, and become cemented to the bone; but the method by which this is effected is still obscure.

The replacement of teeth in venomous snakes is interesting and complex. In the Cobra, an example of the group *Proteroglypha*, where the front teeth on the maxilla are deeply grooved for the transmission of the poison, the fangs, which are of no great length, are vertical and anchylosed to the bone, and when the snake strikes its victim, the teeth are occasionally broken off. A single series of successional poison fangs in different stages of formation lie concealed in a fold of mucous membrane, behind the poison tooth, and in case of injury a tooth moves forwards and occupies the place of the tooth that was lost.

In the Viperine snakes, a still greater development is attained,

the very long poison fangs, anchylosed on either side of the upper jaw, are by their great length peculiarly liable to injury, and are often broken off. In this case, however, a double set of reserve fangs exist, in various stages of development, similarly protected by a fold of connective tissue ; and first from one row, and then from the other, the completed poison tooth moves forward and becomes attached to the bone, the surface of which has been prepared for its reception.

The maxilla is so reduced in size, that there is only room for the poison fang, with a similar space by its side, to accommodate another tooth in case of accident (see Fig. 188).

CHAPTER IV

DEVELOPMENT OF THE TEETH

The Primitive Dental Lamina.—At about the 34th to the 40th day of intrauterine life, before ossification has commenced, when the embryo is about 12 mm. in length, there occurs a proliferation of the cells of the deeper layers of the oral epithelium all round the margins of the future jaws. This multiplication of the cells of the rete Malpighii results in the formation of the Primitive Dental Lamina, which by its encroachment upon the submucous tissue, and the growth of the latter around the lamina, causes the appearance of a groove in the connective tissue when the epithelium is removed.

The Labio-Dental Lamina and Tooth Band.—At the 48th day, according to Röse, the Primitive Dental Lamina divides into two portions. The Labio-Dental lamina turns perpendicularly into the jaw and is destined to form the lip furrow; while the Dental Lamina, or Tooth Band, passes horizontally backwards and upwards in the maxilla, backwards and downwards in the mandible. There exists some difference of opinion as to the relationship of the tooth-band and the labio-dental lamina, some authorities holding that the former is an offshoot of the latter, others that the lip-furrow is a process developed from the tooth-band, while others maintain that they arise separately but at the same time. The latest and currently accepted opinion is that they have common origin from the primitive dental lamina as described above. From the free edge of the tooth-band, which is continuous all round the jaw, the ten germs of the deciduous teeth will be developed in each jaw. The germs appear as thickenings or buds on the labial surface of the band near, but not quite at its free margin.

The cells on the periphery of the tooth-band are columnar

like those of the deeper layers of the surface epithelium, while those of the interior are polygonal in shape.

While this activity is taking place in the epithelial cells, there are some manifestations of changes in the mesodermal cells immediately adjacent to those parts of the tooth-band where the buds of the deciduous teeth are appearing. There is a concentration of embryonic cells in these positions, the number of cells being greatly increased, and some of the round cells take on a fusiform shape with oval nuclei.

The "buds" for the enamel organs of the deciduous teeth appear about the 60th to the 70th day of fœtal life. The cells proliferate rapidly and soon the enamel organ has assumed a form which is usually described as that of a Florence flask. The development of the dentine germ causes a rapid growth of the sides of the base of the flask to embrace the germ, the growth being upwards in the maxilla, downwards in the mandible.

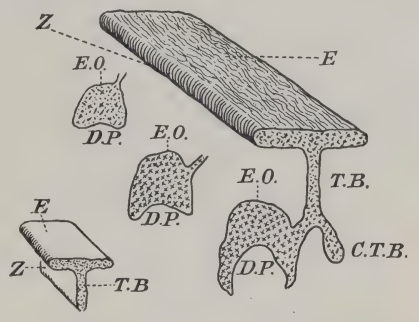


FIG. 58.—Diagrams showing formation of the tooth-band, the relation of the deciduous tooth germs to the tooth-band, and the continuation of the latter to the lingual side of the developing tooth to form its permanent successor.

(Adapted from Hopewell-Smith's *Normal Histology of the Mouth*, after Stohr.)

E, Surface epithelium; *T.B.*, Tooth-band in section; *Z*, Side view of tooth-band as a continuous sheet; *E.O.*, Enamel organs of deciduous teeth; *D.P.*, Dentine papillæ; *C.T.B.*, Continuation of tooth-band to lingual side of the deciduous germ to form the tooth germ of the permanent tooth.

The enamel organ is now the shape of a bell with a handle, and receding from the tooth-band is connected with it by a double row of cells which eventually atrophy and sever the connection.

The outer surface of the organ at this stage is at first smooth, but soon becomes irregular by the formation of papillæ-like structures in the surrounding connective tissue, which project into and indent the external layer of epithelial cells. These papillæ would appear to have some relation to the blood supply of the enamel organ. The cells on the periphery at this stage are similar to those of the deepest layers of the rete Malpighii with which they are continuous, the interior of the organ being occupied with round cells with prominent nuclei.

Meanwhile the mesoderm cells in proximity to the expanded portion of the enamel organ proliferate rapidly, and about the 70th day the condensation of the mesodermal tissue at points corresponding to the enamel organs indicates the first appearance of the dentine germs of the deciduous teeth.

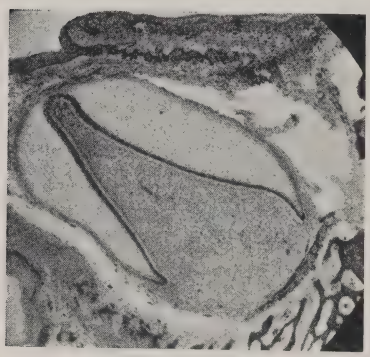


Fig. 59.—Developing tooth of fœtal calf before commencement of calcification. × 30.

The successional tooth is developed by the continued growth of the free end of the tooth-band more deeply into the tissues lingually to its predecessor, followed by the appearance of the enamel bud of the permanent tooth on the labial surface of the band near its free end, as has been described for the deciduous tooth.

The enamel organ of the first dentition is said to be detached from the tooth-band when the enamel bud of the successional tooth appears (Leche); and while the tooth-band maintains connection with the surface epithelium and grows on past the most recently formed tooth germ, there is still a likelihood of tooth formation.

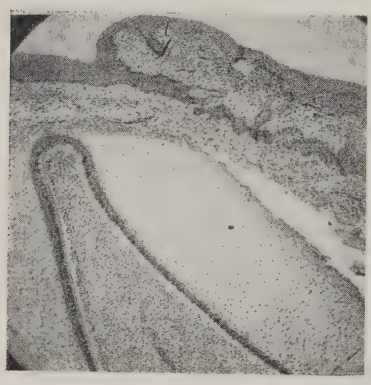


Fig. 60.—Higher magnification of preceding figure, showing the downward growth of the tooth-band to form the permanent tooth. × 40.

At the stage where the enamel organ of the deciduous tooth has assumed a "bell" shape, a shallow furrow has appeared on the free surface of the epithelium over the tooth-band. This is known as the "primitive dental groove or furrow," and is on the top of the jaw in the incisor region, elsewhere on the outer side.

The Stellate Reticulum.—The cells in the interior of the enamel organ now assume a stellate form with long, branching,

interlacing processes, making a complicated network known as the "stellate reticulum." This change into the stellate form commences in the centre of the tissue, and progresses towards the periphery, but stops short at the columnar cells which form the external epithelium. The processes of the cells near the latter are short and not very conspicuous. Between the stellate reticulum and the columnar cells which lie adjacent to the dentine germ are several layers of rounded unaltered cells which are known as the stratum intermedium and are in relation to the columnar cells on the one hand, and the stellate reticulum on the other.

Little is understood of the functions and method of transformation of the cells of the stellate reticulum. Some observers consider that they are undergoing colloid degeneration, and compare them to the degenerating cells in epithelial odontomes, in which the appearances are precisely similar.

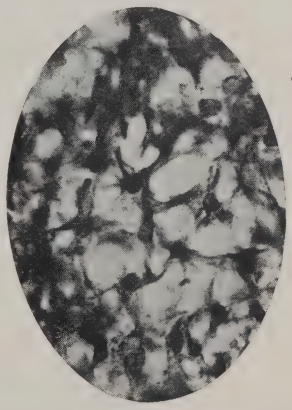


Fig. 61.—Cells of stellate reticulum, showing dark nuclei and branching cells. Silver preparation. × 320.

Others believe the stellate form to be due to the persistence of an intercellular substance from the spaces of which the cells have been washed out in the process of preparation. A modification of this view is that the whole appearance is artificial, due to the action of heat and reagents during preparation, upon the exceedingly delicate cells and intercellular substance which form the body of the enamel organ.

There is no doubt, however, that in properly prepared sections large branching cells can be seen in the stellate reticulum, whose processes, some broad, some fine, communicate with one another. The spaces between the cells are filled with a structureless material which apparently is coagulated by the fixative and takes a faint stain.

At this stage, about the 100th day, the enamel organ is still bell-shaped, the concavity of the bell being occupied by the dentine germ.

The necks of the organ are greatly elongated, the stellate reticulum has attained its greatest development, the dentine

germ is rapidly consolidating and the first appearance of capsule formation is seen.

The cells on the periphery of the enamel organ which lie

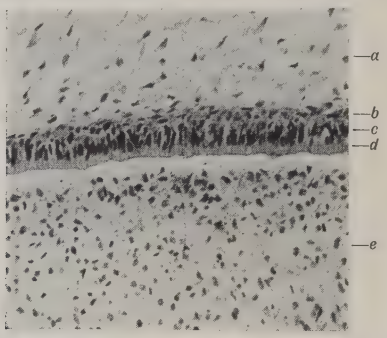


FIG. 62.—A portion of fig. 60, showing the stellate reticulum (*a*), stratum intermedium (*b*), the ameloblasts (*c*), the internal ameloblastic membrane (*d*), and the condensation of the cells on the surface of the dentine papilla before the differentiation of the odontoblasts (*e*). × 160.

nearest the dentine germ now become elongated, and their nuclei recede to the end of the cell farthest from the dentine germ. These prominent columnar cells form a single row, like

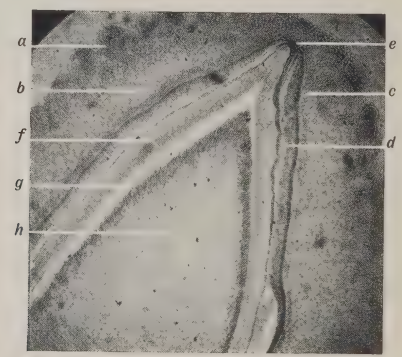


FIG. 63.—Early stage of human tooth germ, just after commencement of calcification. *a*, external epithelium ; *b*, stellate reticulum ; *c*, stratum intermedium ; *d*, internal epithelium ; *e*, formed enamel ; *f*, formed dentine ; *g*, odontoblasts ; *h*, dentine papilla.

a palisading on the internal surface of the enamel organ and are known as the "internal epithelium," "enamel cells," "enamel epithelium," "adamantoblasts" or "ameloblasts." They are largest over the apex of the papilla, dimin-

ishing in size as they pass towards its deepest parts. They are said to rest on a delicate basement membrane.

Structure of Enamel Organ.—The fully-developed enamel organ is therefore made up of four distinct parts, which, proceeding from without towards the interior are—

1. The external epithelium—several layers of rounded, flattened cells.

2. The stellate reticulum—comprises the interior of the organ, and is made up of branching cells with prominent nuclei.

3. The stratum intermedium—six or seven rows of rounded nucleated cells.

4. The internal epithelium —elongated columnar cells with a prominent nucleus at their distal extremity.

The external and internal epithelia are continuous at the deepest part of the enamel organ, and are still connected with the tooth-band by the neck of the enamel organ, and through that structure with the "rete Malpighii."

At about the 120th day the common tooth-band begins to show signs of degenerate changes, becomes fenestrated, and has the appearance of being broken up. This only occurs where the germs are well advanced. Where more teeth are still to be formed, as at the back of the mouth, and upon the lingual side of the deciduous teeth, it remains a complete sheet.

These changes take place also in the attenuated necks of the enamel organs by which the germs are attached to the common lamina. Many of the cells atrophy and disappear, but little islands of epithelium remain, proliferate somewhat, and are known as the "*glands of Serres.*" Mummery has shown, however, that some of the cells of the necks of the enamel organ are responsible for the development of epithelium in the connective tissue of the tooth-follicle. It is from the remains of these that the epithelial "rests" of the periodontal membrane are developed, whose further development under the stimulus of inflammatory changes in the membrane may give rise to cystic or malignant growths.

Dentine Germ.—The dentine germ, which, as we have seen, first appears about the 70th day as an opacity in the mesodermic tissue beneath the developing enamel organ, begins to develop rapidly as the latter attains its mature form. It has been said that the opacity which eventually becomes the dentine germ is continuous all round the jaws, like the dental

lamina from which the enamel organs are formed, and that further development takes place only at points opposite the epithelial proliferations, the intervening portions becoming absorbed.

The round, unbranched, embryonic mesoderm cells have prominent nuclei, and are supposed to be embedded in an

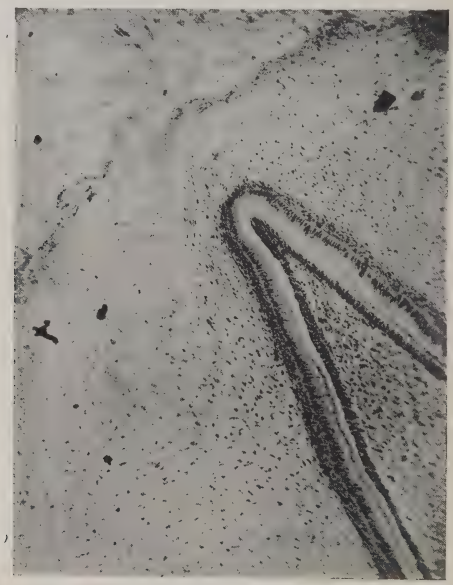


FIG. 64.—Portion of tooth germ of fœtal calf just as calcification of enamel is about to commence.

indefinable matrix. From the base of the germ prolongations of mesoderm tissue are said to grow upwards to embrace at first only the free edge of the enamel organ, and ultimately at a later period the whole tooth germ. From these prolongations the dental sac or follicle is formed, also the cementum and periodontal membrane. Thus the dentine germ and the tooth follicle have a common origin from the mesoderm, while the enamel organ is purely ectodermic.

Sheath of Hertwig.—It is held by many authorities that the primary function of the enamel organ is the determination of the form of the future tooth, and even that the formation of enamel is a secondary function taken on later. A downward growth of the internal and external epithelia of the enamel organ has been described in many mammalian orders (rodents,

ungulates and carnivora for example) which embraces the whole of the roots of the teeth, and is known as the "Epithelial sheath of Hertwig." This is said to determine the form of the root and limit the deposition of dentine. Where there is no Hertwig's sheath there are no odontoblasts and no formation of dentine. The presence of this sheath has not hitherto been demonstrated in human teeth, but has been deduced from its occurrence in the lower orders, and the "epithelial rests" in the human periodontal membrane.

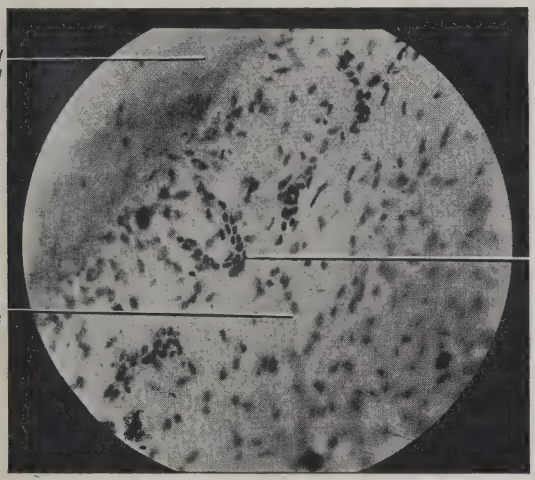


FIG. 65.—Periodontal membrane of human mandibular molar, showing the remains of the Sheath of Hertwig near the end of the root. Cut *in situ*. Stained Hæmatein and Van Gieson. × 160.

In this connection Mummery's preparations carry our knowledge a step farther.

He shows that the sheath is not formed in the manner described already as a downgrowth of the enamel organ, but is shut off from the latter in the connective tissue of the tooth follicle. The enamel organ itself is not prolonged beyond the neck of the tooth, but ceases where enamel formation ceases.

The cells of which the sheath are composed are derived from epithelial cells which are very abundant in the coronal part of the follicle.

He considers that they arise from "proliferations of the tooth-band within the follicle and also from buddings or proliferations of the external epithelium of the enamel organ,

with which the epithelial cells of the follicle form connections."

The sheath will be more fully dealt with in the description of the tooth follicle.

The phenomena so far described refer principally to mammalian orders, and particularly to the human dentition. In lower vertebrates there is much that is common with the higher, such differences as exist being chiefly concerned with the arrangements for the development and protection of the successional teeth.

Elasmobranch Fishes.—A vertical section of the jaw of the dog-fish (*Scyllium canicula*) will show the analogy between

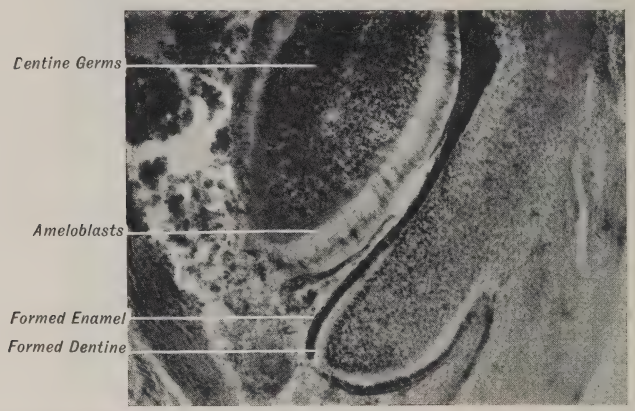


Fig. 66.—Successional teeth of Dog-fish, showing the internal epithelium of the enamel organ. × 50.

the dermal spines of the lip and the teeth, the latter being nothing more than enlarged spines. Both are identical in form, and their manner of attachment by a broad expanded base in the soft submucous tissue is the same in each case. The successional teeth are placed on the inner surface of the jaw and are shown in varying stages of development, the youngest tooth germ lying in the deepest part of the tissue, the others increasing in maturity until the functional tooth in position on the margin of the jaws is reached.

The tooth germs are protected by a reflection of the mucous membrane of the mouth called the thecal fold. This is not a free flap forming a ditch with the opposite surface, in which lie the successional teeth, but is a growth, upwards or downwards, of connective tissue, covered on its free surface by epithelium

which is continuous with the epithelium on the surface of the jaw. The only epithelium present in the developmental area is that of the continuously growing tooth-band.

The enamel organ in the dog-fish consists of a pronounced layer of elongated columnar cells with well-marked nuclei which cover the surface of the dentine germ, the remainder of the organ being composed of much smaller cells with intercommunicating processes. All the enamel organs present are held in continuity by this tissue, but the columnar cells in the intervals between the developing teeth atrophy.

The dentine germs are clearly seen to arise from the connective tissue immediately beneath the columnar epithelial cells, there being no sharp line of demarcation to distinguish the base of the germ from the surrounding mesodermic tissue, but a gradual transformation from the large round cells of which the dentine germ is composed, to the more fibrous elements of the mucous membrane, which again are gradually transformed into the densely fibrous gum on the surface of the jaw.

Thus there are no follicles in the order Selachii.

In structure each adult tooth is composed of a body of hard fine-tubed dentine with a central pulp chamber.

The pulp is composed chiefly of numerous round cells in a fibrous matrix, and is fairly well supplied with blood-vessels, which enter the pulp by an aperture at the side of the expanded base of the tooth.

There is a thin superficial covering of so-called enamel. This is the tissue which will be described later on in Chapter VI.

Teleostei.—In the osseous fishes there is no tooth-band, each tooth germ being developed independently from the oral epithelium, having no connection with a tooth-band or with the germ of the preceding tooth.

A proliferation of the deeper cells of the oral epithelium forms the enamel organ, which invests the dentine papilla "like a cap." If there is to be no enamel, or only a rudimentary layer formed, the cells of the enamel organ will not become further differentiated; but where a tip of enamel is to surmount the tooth, the enamel-forming cells will develop to a great size (as in hake, *Merlucius vulgaris*) in the area where the enamel is to be deposited, while elsewhere the cells of the enamel organ remain small and insignificant.

The stellate reticulum is rudimentary, consisting only of strands of fibres with no cells. The odontoblasts in some specimens are not distinguishable from the other cells of the pulp except for their position.

There is no dental sac.

Amphibia and Reptilia.—In these creatures the enamel organ is developed from a tooth-band, and the dentine germ from the submucous tissue, as has been described for Elasmobranch fishes and Mammals, the chief points of difference being in the relation of the successional tooth germs to each other.

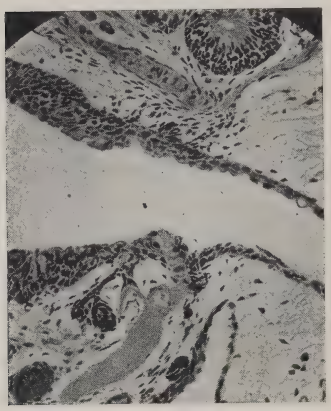


Fig. 67.—Tooth-band and successional tooth germs of Newt—lower jaw. First appearance of dental lamina in upper jaw. × 80.

In the newt (*Triton vulgaris*) the jaws are extremely thin and delicate.

The tooth-band grows down from the epithelium near the free margins of the bone. It is shallow and flat and grows continuously towards the median line on past the latest germ which is formed from its side near the growing end.

The tooth-germ is of the simplest form, consisting only of an enamel organ and a dentine germ. The cells of the enamel organ are large, the teeth being surmounted with an enamel tip like those of the eel. In the frog the edentulous lower jaw closes inside the upper jaw, on the margins of which are developed a row of insignificant teeth. This so constricts the area of tooth-development that it has not yet been ascertained whether the successional teeth arise from a tooth-band, or *de novo* from the surface epithelium. The new tooth-germs of the lizard are developed deeply in the tissues at the floor of the area of tooth development. This has the effect of lengthening the neck of the enamel organ greatly as in the case of the newt.

The teeth are more completely covered with enamel than are those of the newt, hence the enamel cells are developed further down the sides of the dentine papilla. There is also

an appearance of a capsule, caused by the condensation of the surrounding connective tissue which occurs as the result of the growth of the tooth.

Certain lizard-like creatures (sphenodon and chamæleon), although having no successional teeth formed, develop a tooth-band to the inner side of the tooth in use.

Ophidia.—In snakes the number of successional teeth in course of development at the same time is more numerous than is the case with other reptiles. Consequently the area of

Fig. 68.—Dental lamina and successional tooth germs of Lizard. × 160.

tooth development is somewhat specialized in these creatures.

The tooth germs are arranged almost vertically and parallel with the surface of the bone of the jaw, and are protected from injury and the possibility of displacement during the expansion of the mouth, by a covering or bag of connective tissue. The tooth-band enters the area of tooth development at the top of the bag, and winds its way amongst the tooth sacs to the bottom of the area where the youngest tooth germ will be found with the free end of the tooth-band.

There is a well-developed enamel organ, with large ameloblast cells, which probably form a thin layer of enamel on the surface of the ortho-dentine of which the body of the tooth is composed.

As the development proceeds the tooth sac assumes a recumbent position, the growing tooth lying parallel to the long axis of the jaw. Such an arrangement obviously prevents injury

during expansion of the jaws. The tooth remains in this position until it moves into place on the summit of the jaw.

Crocodilia.—The tooth-development in crocodiles is similar to that of Mammals and needs no special description. The successional teeth occupy the same socket as their predecessors.

CHAPTER V

DEVELOPMENT AND CALCIFICATION OF ENAMEL, DENTINE AND CEMENTUM

Development of Enamel

It will be convenient to describe the development of the individual tissues from the point of the commencement of calcification.

The enamel organ is still connected to the tooth-band by a very attenuated neck. The ameloblasts over the point where calcification is to commence have assumed their characteristic shape and some odontoblasts have developed opposite them on the surface of the dentine papilla.

At this time, about the 140th day, the first deposition of dentine occurs in the dentine papillæ of the deciduous incisors, the enamel appearing immediately afterwards.

The materials from which enamel is formed are brought to the outer surface of the enamel organ in the blood stream, and are there selected and passed through the various cellular layers and finally deposited as the completed tissue. Exactly what the process is, and what are the functions of the cells, have not yet been ascertained.

The following views embody all the most recent work on the subject.

External Epithelium.—It was for long thought that the external epithelium had no particular function beyond that of limiting the extent of the enamel organ, but now the generally accepted view is that it is concerned with the separation of certain constituents of the blood which are needed to form enamel. These constituents are further elaborated by the cells of the internal epithelium.

The papillary projections which have been described in connection with the external epithelium are not secreting

papillæ, as has been suggested, but are for the accommodation of the blood-vessels of the capsule which convey nutritive material in solution to the stellate reticulum.

The blood-vessels of the capsule are in close relationship with the external epithelium and sometimes breaks of continuity in the latter reveal blood-vessels in contact with the stellate reticulum. In some Marsupials Mummery and others have described blood-vessels crossing the external epithelium and entering the stellate reticulum. This is a common condition in the rat.

Epithelial buds arise from the outer surface of the layer which proliferate within the tooth follicle and from which it is possible that Hertwig's sheath may be developed. The ultimate fate of the cells of the external epithelium is to become incorporated with other cells of the enamel organ as the outer layer of Nasmyth's membrane.

Some observers contend that the external epithelium is atrophied before the enamel is completely calcified.

Stellate Reticulum.—The functions of the stellate reticulum are unknown. There are two theories.

One regards it as a packing material to fill up space subsequently occupied by the growing tooth.

The other looks upon it as a storehouse for calcific material.

Whatever its functions, it is quite certain that its presence is not essential to the formation of enamel, for it is absent from the enamel organs of fish and reptiles and disappears in mammals long before the tissue is complete.

Stratum Intermedium.—The cells of the stratum intermedium before the commencement of calcification are close to the ameloblasts and often between the distal ends of those cells. After calcification has begun they are separated from the ameloblasts by the external ameloblastic membrane. Some of them lose their round form and become somewhat flattened.

They are connected by processes with the cells of the stellate reticulum, and according to Tomes with a basal process of the ameloblasts. After the disappearance of the stellate reticulum the cells of the external epithelium come to be in contact with the stratum intermedium, bringing the blood-vessels of the capsule close to the latter structure.

Williams has described papillæ-like projections in the

stratum intermedium of the rat, which he claims to be true secreting papillæ. The functions of these cells are unknown.

It was thought at one time that they recruited the ameloblasts as they got exhausted, or where additional cells were required to cover a larger area. The existence, however, of a membrane between the stratum intermedium and the internal epithelium would prevent any such arrangement. It is probable that they are concerned in the elaboration of material for the ameloblasts to use in their work of enamel formation.

Ameloblasts. — The ameloblasts are the actual enamel builders and are constantly present wherever enamel is found, even when the remaining parts of the enamel organ may be absent.

They are large columnar cells with prominent nuclei usually at their distal extremities.

Fig. 69.—Developing tooth, human fœtus, showing cells of stratum intermedium (S.I.), ameloblasts (A.), internal (I.M.) and external (E.M.) ameloblastic membranes. Tomes' processes (T.P.), formed enamel (f.e.), formed dentine (f.d.), odontoblasts (O), odontogenic zone (Od.), and dentinal fibrils (D.F.) *in situ*. × 320.

They measure 5 μ across and from 15 to 20 μ long. The length varies of course with the period of activity, and also apparently with the amount of tissue that has to be deposited. The nuclei are large and round, with well-marked nucleoli, and a "fine reticular structure and granules of chromatin" can be seen.

The position of the nucleus, as already mentioned, is generally at the end of the cell farthest from the enamel, but it can frequently be seen nearer the enamel.

Angular or square nuclei are sometimes present and at times a crescentic form is seen with the horns of the crescent towards the enamel. Mummery shows figures in which the horns of the crescent appear to be attached to delicate fibres or plasmic threads which are continuous with the fibres of Tomes' processes.

The cells have delicate lateral membranes which are very

difficult to demonstrate but can be made out in suitable preparations.

They are said to be in actual contact, although it has been claimed that a space exists between each cell equal in width to the channel of interprismatic material in the enamel. This statement awaits confirmation.

Ameloblastic Membranes.—According to some observers there are no membranes at either end of the cells. This may be true before the commencement of calcification.

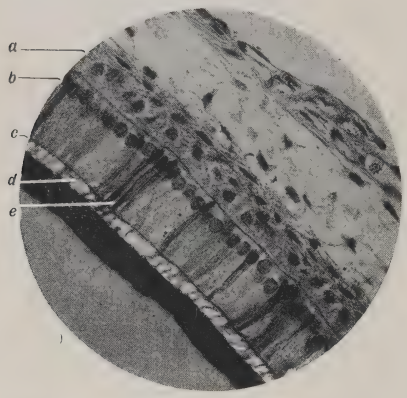


FIG. 70.—From developing tooth of kitten—secreting ameloblasts. Preparation stained with Mann's methyl-blue-eosin. Section kindly lent by Mr. Griffiths. × 300.

a, cells of stratum intermedium; *b*, external ameloblastic membrane; *c*, internal ameloblastic membrane; *d*, Tomes' processes; *e*, secreting cells.

Huxley, however, described a kind of basement membrane, which he called the "membrana preformativa," which lay at first between the ameloblasts and dentine papilla, and afterwards between the ameloblasts and the formed enamel. This is probably identical with what has since been described by Williams as the "internal ameloblastic membrane." Between the ameloblasts and the cells of the stratum intermedium, as soon as calcification is about to commence, there appears another delicate membrane, the "external ameloblastic membrane," which definitely separates the two layers.

Both the external and internal membranes are structureless and continuous over the entire layer of ameloblasts, and are looked upon as dialyzing membranes, through which lime salts in solution pass to be "fixed" by some substance on the other side of the membrane.

The cytoplasm of the ameloblasts is granular, and during the period of cellular activity contains clear oval bodies of variable size, the "*enamel globules*" of Williams, which are secreted by the cells and which by their fusion are said to form the enamel rods.

Protoplasmic Fibrils.—Passing down the cells from the internal end of the cell towards the nuclear end are the delicate protoplasmic fibrils or "plasm-strings" already mentioned. These would appear to be in connection with the nucleus, and according to Mummery pass into Tomes' process, and from the process are incorporated in the forming enamel.

Tomes' Process.—When active enamel cells are pulled away from the surface of forming enamel, as often happens in cutting sections of developing teeth, a tapering process or prolongation of the cell is to be seen jutting out of the enamel end. This is known as "Tomes' process." It is especially distinct in marsupial enamel, in some creatures being nearly as wide as the cells.

Mummery claims that the process is finely fibrous in structure, the fibrils being continuous with the "plasm strings" in the ameloblasts.

The processes are incorporated with the substance of the forming enamel, and with "other transversely arranged fibres" form the organic framework of the enamel. The calcification of the prisms takes place in this "fibrillar basis substance."

The Honeycomb.—On the surface of forming enamel there is a conspicuous honeycomb appearance which Tomes first described in Marsupials.

It is a tissue on the border-land of calcification, identified by Tomes with the fenestrated membrane which can always be obtained from the surface of forming enamel.

Tomes' processes are said to occupy the centre of the spaces in the comb. Calcification commencing in the septa and proceeding towards the centre completely obliterates the space in non-tubular enamel, but stopping short of the centre leaves the channels occupied by living plasm as seen in marsupial and other tubular enamel.

If this view is correct it would mean that there is no real interprismatic cement substance, and that the connection of the contents of the enamel tubes with the dentinal fibrils is a secondary affair.

Mummery looks upon the honeycomb as a transitory substance. He describes the fibres of Tomes' processes as spreading out fan-wise in this region, "crossing one another and intermingling, to be again drawn together to form the columns of

the prismatic substance of the enamel." Thus the fibrillar scaffolding of the prism is not the product of one ameloblast but of several neighbouring cells.

Calcification of Prisms.—According to this view calcification commences at the centre of the prism and proceeds outwards, and the rods and the cementing substance are derived from independent sources.

Mummery has shown in teased preparations of forming enamel that the tissue breaks up in distinct laminæ parallel to the surface, and that on and between the laminæ large radial calcospherites can be seen. Smaller globules of calcific material he also describes as in the substance of the rods.

He concludes that the large bodies are concerned with the formation of the cement substance, and the small globules he identifies with those already described in the ameloblasts which pass through the internal ameloblastic membrane, arrange themselves along the fibres and become fused as calcified granules to form the enamel rod.

The most recent work on the calcification of the enamel leads to the conclusion that the enamel is elaborated by the activity of the ameloblasts from material which is selected, prepared, and perhaps stored by the other parts of the enamel organ. That, so far as the rods are concerned, there is a "fibrillar basis substance" derived from the fibrils of Tomes' processes.

The interprismatic cement substance is formed independently. There are two kinds of calcospherites concerned in the process: the small regular globules of the prisms and large radial spheres which break up into small granules or become fused. In either case the calcification of the cement substance is brought about by their agency.

The large spheres are such as are formed when solutions of calcium carbonate have been used in dialyzing experiments, and it is possible that in the early stages of the calcification of bone, dentine, and enamel, carbonates are in excess; or alternatively, that the carbonate radicle in the combined salt said to form the basis of the inorganic constituents of enamel, and other calcified tissues, may induce the large globular formations seen in the calcification of those tissues.

Tubes in Marsupial Enamel.—The views as to the nature of the tubes in marsupial enamel involve different conceptions as to the formation of that tissue.

Tomes' view that the tubes are simply the uncalcified central portion of the prisms has already been mentioned, from which it follows that calcification of all enamels commences at the periphery of the prism and proceeds towards the centre.

Mummery's view in opposition to this is that the tubes are not in the prisms but between them, that they are true dentinal tubes that have grown from the dentine in the uncalcified cement substance of the enamel. That calcification of the prism takes place centrifugally and that the cement substance is developed independently.

Development of the Enamel in Fish.—There is much speculation about the nature of the tissue which forms a cap or a complete covering for the teeth of many fish.

In Elasmobranchii, before calcification has begun, a layer of some thickness is developed on the surface of the pulp. This is composed of spindle-shaped cells with very long processes. Calcification of the dentine takes place beneath this layer, soon cutting it off completely from the pulp. This forms the mesodermic matrix into which the ameloblasts pour their secretion. The enamel of these creatures then is derived partly from the ectoderm and partly from the mesoderm, and zoologists are generally loth to classify it as enamel.

In some teleosteal fishes, as for instance the Gadidæ, enamel is developed only on the tip of the tooth, forming a sharp point.

When calcification of the dentine is about to commence the ameloblasts elongate enormously and finally disappear. The space above the growing dentine cap which will ultimately be taken up by enamel, is filled with a stroma with elongated meshes which looks like delicate connective tissue. In transverse section, the tissue is marked with regular perforations. The enamel is deposited in this tissue apparently without the aid of any special cells so far as is known.

Blood-vessels are abundant in the capsule but do not enter the enamel organ.

An investigation of the development of enamel in the Sparidæ and Labridæ has recently been undertaken by Mummery. He finds that at first the enamel organ consists of ameloblasts and external epithelium.

A thin layer of enamel is laid down by the ameloblasts, which then disappear, their place being taken by a delicate

stroma within which a special secreting apparatus is developed.

Parallel tubes appear in this stroma at right angles to the surface, stopping just short of the forming enamel. Some of the tubes contain blood-vessels which are in communication with the vessels of the capsule. Alternating with these are secreting tubes. Between the blood-vessels and the secreting tubes there is a delicate tissue amongst which are numerous rounded cells with prominent nuclei.

The secreting tubes do not reach the capsule but end between two of the vascular tubes. The inner end is continuous with the stroma above the forming enamel.

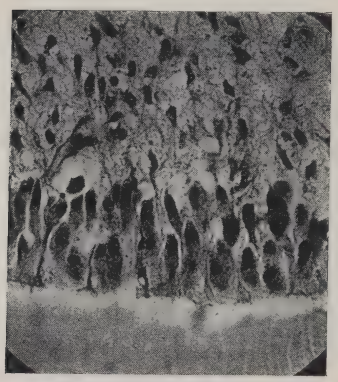


FIG. 71.—Odontoblasts from the developing tooth of a kitten. × 300.

The lime salts are probably separated from the circulating blood by the above-mentioned cells, whence they pass through the secreting tube to the forming enamel.

This arrangement was found in Sargus ovis, whilst modifications of it were found in certain of the Labridæ—Tautoga onitis, Halichœres and Pseudolabrus.

The remains of these tubes are seen in the finished tissue passing into the enamel from the external surface.

DEVELOPMENT OF DENTINE

Odontoblasts.—The first indication of differentiation of the cells of the dentine papilla is the appearance of large rounded cells at its margins. They have large nuclei and little cytoplasm, but no processes. They soon become pyriform in shape, and develop a process from their outer end which eventually becomes the dentinal fibril. These are the odontoblasts.

The old idea that dentine was formed by the conversion of the odontoblasts into calcified matrix, leaving the soft uncalcified central portion as the dentine fibril, has been largely abandoned. At the present time the majority of histologists accept the secretion theory, which is that certain

pulp cells secrete a material which calcifies, and that the cells on the surface of the papilla recede as the dentine grows, leaving in the dentinal tubules a process—the dentinal fibril.

Connective Tissue Matrix.—The calcification takes place in the connective-tissue matrix or ground substance of the pulp. Mummery first called attention to the fibres at the edge of and passing into the forming dentine, and Von Korff and others have since described corkscrew-like fibres passing between the odontoblasts in developing dentine, which the former looked upon as proof that the dentine was not a product of the odontoblasts but of the connective tissue of the pulp. Bundles of gelatine-yielding fibres are also described analogous to the penetrating fibres of Sharpey in bone.

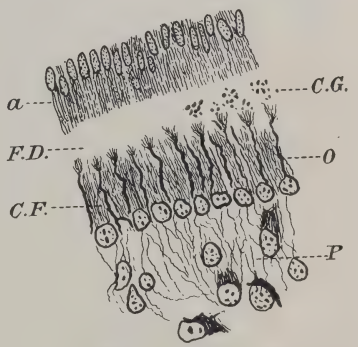


Fig. 72.—Fibres of Von Korff passing across the odontoblast layer and becoming incorporated in the forming dentine. Tooth germs of a Cat.

a, Ameloblasts; *F.D.*, Forming dentine; *O*, Odontoblasts; *P*, Pulp; *C.F.*, Corkscrew fibres of Von Korff; *C.G.*, Calcific granules. (After Von Korff.)

The part played by the odontoblasts in the formation of dentine is still a matter of dispute. Hopewell-Smith looks upon the term odontoblast as a misnomer, these cells not being concerned in the deposition and calcification of dentine. He considers that they are "actual end organs or dental ganglia of the nerves of the pulp." The active agents in the process of dentine building are according to him the small round cells of the pulp.

It is now, however, generally accepted that odontoblasts preside over and direct the process, and that they secrete the calcific material into a fibrous matrix laid down to receive it.

Pulp Cells.—Under special conditions other pulp cells can also lay down a dentine-like substance such as one sees in calcareous degenerations of the pulp. Calcification takes place by the dialysis of lime salts into the collagenous matrix, small globular bodies appearing which fuse to form larger *calcospherites*. Interglobular spaces show these rounded forms very distinctly. The globular bodies are at first structure-

less but soon become laminated with concentric markings. Later on the calcospherites become disintegrated, the concentric markings being stretched out into parallel lines which are preserved in the young dentine as faint laminæ more or less parallel to its surface.

It is thought that the diffusion of lime salts takes place from the dentinal fibril through Neumann's sheath into the surrounding tissue.

Mummery points out that the calcospherites of forming enamel have radial striæ, while those of dentine have concentric markings.

FIG. 73.—Calcospherites.

a, connective form (formed in albumin); *b*, radial form (formed in albumin); *c*, radial spherite from marsupial forming enamel; *f*, similar to *c*, disintegrating; *d*, oval spherite from human developing enamel; *e*, granular spherite from human enamel.

(From Mummery's *Microscopic Anatomy of the Teeth.* Oxford Medical Publications.)

Vaso-dentine.—In the development of vaso-dentine the blood-vessels at the periphery of the pulp, instead of receding as calcification advances, as is the case with ortho-dentine, become surrounded by calcifying matrix and are finally incorporated in the completed tissue.

The connective tissue of the pulp is very abundant, and on its surface in the position usually occupied by odontoblasts, there is a distinct layer of coarse fibres, which have been looked upon as odontoblasts. Amongst them are seen rounded cells having much the appearance of osteoblasts.

The presence of the odontoblasts would appear to depend upon the existence of tubules in the dentine, as in those teeth which have tubular dentine in one part and vaso-dentine in another, odontoblasts are found in the pulp tissue beneath the tubular portion but are absent lower down.

Osteo-dentine. — The development of osteo-dentine is exactly similar to that of bone in membrane.

In the other varieties of dentine the tissue is formed on the

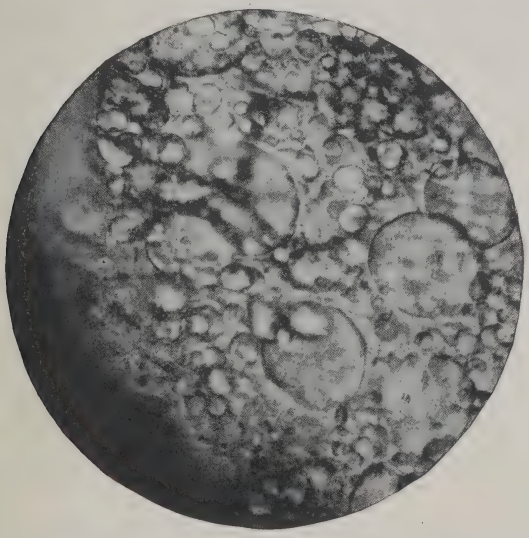


FIG. 74.—Mass of calcospherites from surface of forming enamel of temporary human molar within the tooth sac. × 600.
(From Mummery's *Microscopic Anatomy of the Teeth.* Oxford Medical Publications.)

surface of the pulp, but in this, except for the narrow external layer, which is developed from a surface layer of not highly specialized cells, the process is quite different.

As soon as the external layer is formed the rudimentary odontoblasts, of which it consists, disappear. The pulp becomes traversed by calcifying trabeculæ, which are continuous, with bundles of connective tissue fibres. Soon there is no central pulp cavity, the tissue being made up of medullary canals of varying sizes, containing pulp tissue, alternating with columns of calcified tissue. There are no odontoblasts, but osteoblasts line the trabeculæ.

Where the teeth are to be anchylosed to the bone connective

tissue bundles pass from the tooth to the bone, and being firmly incorporated in both tissues form a very firm union.

Development of Cementum

Cement Organ.—In Herbivora and animals possessing thick coronal cementum a special cartilaginous cement organ has been described, but where the tissue is confined to the roots, as in human teeth, the process is like that of membranous bone. Prior to its formation the connective tissue of the follicle is separated from the dentine of the root by the epithelial prolongation known as the sheath of Hertwig, which is said to mould and limit the deposition of dentine. When the deposition of cementum is about to begin, connective tissue bundles pass from the follicle wall between the cells of the sheath to the dentine, breaking up the sheath into individual collections of cells.

Cells exactly resembling osteoblasts accompany the fibres and are distributed in spaces between the connective tissue bundles. The latter are incorporated in the cement as Sharpey's fibres. Some of the osteoblasts get incorporated in the calcified matrix just as in bone, and with their processes form the cement lacunæ and canaliculi.

They are considered to be "specially modified connective tissue corpuscles, perhaps of the nature of plasma cells" (Schafer).

It was thought at one time that the osteoblast was actually converted into bone or cementum, but the generally accepted view now is that the cells secrete a material which calcifies.

Sharpey's Fibres.—The nature of Sharpey's fibres is not known. They usually extend right across the tissue from the periodontal membrane to the granular layer in the dentine and pin the laminæ together, binding the tissue to the dentine. Some authorities look upon them as being uncalcified fibres imbedded in a calcified matrix. Others regard them as elastic in character, while others again believe them to be fully calcified.

In caries of the cementum micro-organisms enter the tissue by the channels in which the fibres lie, exactly as dentine is attacked via the dentinal tubes.

The Tooth Follicle.—The tooth follicle, the tooth-sac or dental capsule is a fibrous bag in which the developing tooth

is enclosed in its bony crypt, and which disappears with the eruption of the tooth.

It is mesodermic in origin and is said to be derived from the dentine papilla by upward growths from its base which meet and completely surround the tooth germ. It is doubtful, however, if such an upward growth from the papilla really occurs, and Tomes considers it more likely that the follicle is

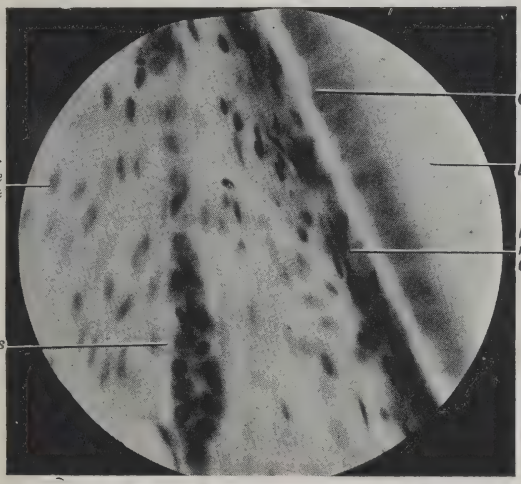


FIG. 75.—Epithelial Cells in periodontal membrane, the remains of the Sheath of Hertwig; from the middle third of the root of a mandibular molar. Prepared and stained as in Fig. 65. × 320.

formed by a condensation of the connective tissue about the germ.

Its functions are to protect the developing tooth, and from it are formed cementum and the periodontal membrane.

It is a tough, whitish membrane, which can easily be detached from the surface of growing teeth before eruption.

When eruption of the tooth is about to take place the cells of the superficial part of the capsule undergo degenerative changes, the tissue becomes vacuolated and finally disappears.

It is made up of bundles of connective tissue fibres which interlace in a very complex manner. The outer portion is less dense than the inner, but there are not two distinct layers.

The cells are few and blood-vessels not numerous.

Development of Epithelium.—The epithelium within the follicle is a matter of much interest.

Mummery has recently studied the follicle of a permanent tooth *in situ*, and he shows that in the coronal portion a continuous development and degeneration of epithelium goes on in the follicle right up to the time of eruption.

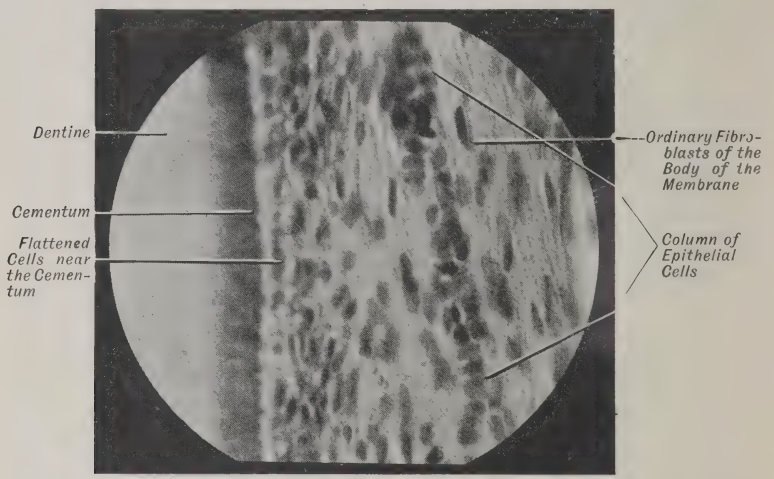


Fig. 76.—Column of Epithelial Cells in the periodontal membrane from the side of a root of a human mandibular molar. Stained as in Fig. 75. × 320.

Cell nests, epithelial coils and multinucleated cells, all signs of degeneration, are to be seen amongst the epithelium here as well as actively growing young epithelial cells.

This development of epithelium, he concludes, comes from buds on the external epithelium of the enamel organ and remnants of the neck of the organ and the tooth-band which have been enclosed in the follicle.

He demonstrates that the epithelial sheath of Hertwig is present in the follicle of the human permanent tooth, and that it surrounds the entire root or roots of the tooth, its probable function being to determine the shape and limit the growth of the tooth. The sheath passes down the forming root, "parallel to its surface, but not in contact with it, and is a more or less continuous band, often arranged as a distinct network, so that the tooth at this stage is enclosed in an epithelial net with open meshes" (Mummery). It is not an extension of the enamel organ proper but a downward growth of the

epithelium, which is developed in the coronal portion of the follicle.

The sheath is eventually broken up by the bundles of connective tissue fibres which go to form the cementum and

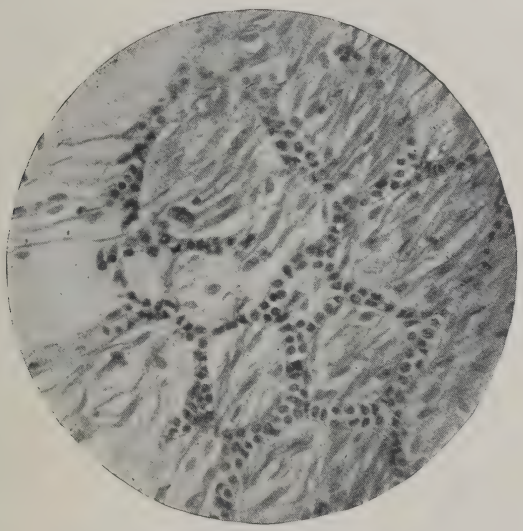


Fig. 77.—Epithelial sheath beneath root in nearly completed tooth. Network of epithelial cells. ×250.
(From Mummery's *Microscopic Anatomy of the Teeth*. Oxford Medical Publications.)

periodontal membrane. The isolated islands of epithelium thus formed either atrophy and disappear or are left in the periodontal membrane as epithelial "rests."

CHAPTER VI

ENAMEL, HUMAN AND COMPARATIVE. NASMYTH'S MEMBRANE

Imbrication Lines.—If the outer surface of the crown of an unworn tooth is examined with the naked eyes or under a magnifying glass, it will be found to show faint parallel markings running transversely to the long axis of the tooth. These markings are alternate ridges and depressions which can be thrown into relief by rubbing the surface with graphite, and have been termed by Pickerill "imbrication lines."

FIG. 78.—Imbrication lines on human enamel. (From G. Fischer's *Bau und Entwickelung der Mundhöle.*)

The ridges are widest and the furrows deepest at the occlusal or incisal third of the tooth. From this point they become less marked, both towards the incisal or occlusal edge and towards the neck of the tooth.

In the cervical region the ridges are narrower, the furrows are closer together and shallower.

Pickerill found that the furrows were 0·01 mm. apart in the cervical region and 0·1 mm. apart in the middle of the crown.

They have been previously described by Preiswerk, from whose work the accompanying illustration is adapted by Guido Fischer. Tomes also describes the outer surface of the enamel.

These furrows are said to be due to the outcrop of the Striæ of Retzius.

The pellicle of Nasmyth's membrane is closely adapted to

the ridges and furrows, the latter being well shown as sinuous lines by impregnation of the membrane in position with nitrate of silver, and its subsequent removal with 5 per cent. hydrochloric acid (see Fig. 102).

Microscopic Anatomy.—A thinly ground section of a human tooth examined under the low power of the microscope will show that it is composed of several distinct structures, which can be readily identified.

Commencing at the neck of the tooth a cap with a milky translucency will be seen to invest the crown, thinnest at the neck where it tapers to vanishing point, and thickest over the cusps, where it has to resist the brunt of the force of mastication. This cap is the *enamel* covering of the exposed surfaces of the teeth.

Fig. 79.—Ground section of human Premolar. × 3·6.

Beneath the enamel, forming the greater portion of the body of the crown of the tooth and extending to the end of the root, is the *dentine*. This also is translucent, but has somewhat different optical properties to the enamel.

In the centre of the section is a cavity occupied by the soft vascular *tooth-pulp* during life.

The size of the pulp cavity varies with the age, being larger in the young than in the adult tooth. In a young tooth 15 mm. long, and 6 mm. in width at the neck, a section cut through the centre of the pulp cavity will show the latter to be 9 mm. in length and 2 in width at the widest part (Fig. 79).

Lining the whole of the root of the tooth and usually in some sort of contact with the enamel is a thin veneer of a clear substance, thinnest at the neck and thickest over the end of the root—the *Cementum*.

Human Enamel, Composition and Structure

Chemical Constitution of Enamel.—The hardest of animal tissues is often described as consisting entirely of inorganic material.

The analyses of C. S. Tomes and Black agree in that they both failed to obtain reactions indicating the presence of organic matter, or only such minute quantities as to be impossible of estimation.

In this respect they differ from the earlier investigations of Hoppe-Seyler and Von Bibra, whose results gave the percentage of organic matter in adult human enamel as 3·59 or 3·60.

Hoppe-Seyler states in addition that infant enamel contained more organic matter than adult.

Von Bibra's analysis is usually given, and is as follows:—

Calcium phosphate and fluoride	89·82
Calcium carbonate	4·37
Magnesium phosphate	1·34
Other salts	0·88
Cartilage	3·39
Fat	0·20

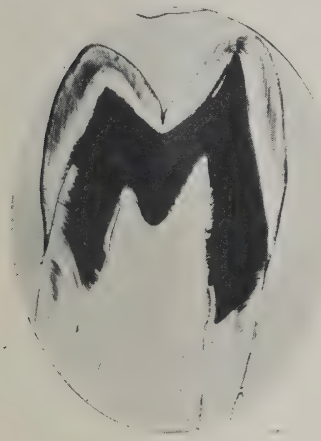
Von Bibra found that organic matter was in greater abundance in the female than in the male, and gives the percentage in the former as 5·97. The most recent work on the problem was contributed by Lovatt Evans and Underwood to the International Medical Congress in 1913. They found in human enamel 1 to 2 per cent. of organic matter which, as Howard Mummery points out, "may be quite sufficient to account for the histological evidences of the presence of organic matter."

As to the nature of the organic basis nothing is known. It is not collagen as in bone, dentine and cementum, but is probably of a mucinous nature.

Distribution.—It forms a covering for the crowns of the teeth of man and most mammals. In *Artiodactyle Ungulata* a thick coating of cementum is developed over the enamel.

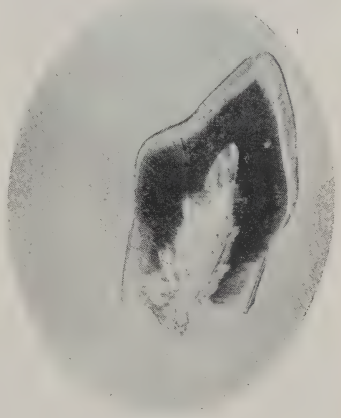
In Rodentia it is developed on the sides and front of the incisors and serves to maintain a cutting edge. For the same reason it is confined to the front and sides of the lower canine of certain bunodonts.

It is said to occur as a tip or point on the teeth of certain fish, e.g. *Merlucius vulgaris* (the hake), *Murœnidœ—Anguilla vulgaris* (the eel), but the structure and composition of this so-called fish enamel is so different from that of the mammalian tissue, that it is doubtful if it can be classed as enamel. It is absent entirely from the teeth of many fish and reptiles, all Edentates and some Cetaceans.



Human Premolar.

FIG. 80.



Human deciduous Canine.

FIG. 81.

Compare the thickness of the enamel in the two specimens and note the shape of the deciduous tooth towards the neck of the crown. × 3·6.

Its thickness varies very much in the individuals of the same species. This variation is particularly well marked in human enamel.

The enamel of the deciduous teeth is in structure identical with that of the permanent set, but is much thinner.

If the enamel is examined by transmitted light under a magnification of 50 diameters, the tissue will show irregular alternations of light and shadow, indicating differences in optical properties which depend in some way upon the completeness or incompleteness of calcification. The more highly calcified the tissue, the more translucent it is. Some of the shadows, such for instance as one gets on the outer surface, are

possibly due to pigment taken into the mouth, or elaborated by chromogenic bacteria adherent to Nasmyth's membrane.

Brown Striæ of Retzius.—Some of these shadow markings run through the tissue more or less longitudinally, in parallel lines, but at varying distances apart. They are known as the "Brown striæ of Retzius," and in some cases are so well marked as to produce an appearance of lamination. They indicate the periodicity of the activity of the enamel-forming cells, each striation being the termination of one period of secretion and the commencement of another. In hypoplastic enamel the striæ are much fewer in number, or absent entirely, while in another part of the tooth, not affected, they may be quite normal in number and appearance.

FIG. 82.—Penetration of enamel from outer surface. Nitrate of silver preparation. Ground section. The brown striæ of Retzius are also well shown. × 40.

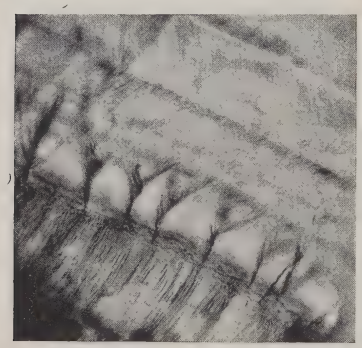
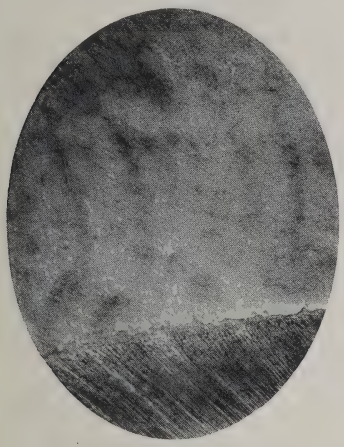


FIG. 83.—Transverse section of the crown of human molar showing the lamination of enamel (the brown striæ of Retzius in section) and the brush-like structures at the margin of the dentine. × 80.

In a transverse section of the middle portion of the crown of a tooth, the brown striæ of Retzius will show as concentric rings in the enamel, parallel to the surface of the dentine and the external surface of the enamel. They divide the tissue into laminæ or layers.

There is some diversity of opinion as to the cause of these lines. Kölliker, Walkhoff, Mummery, Pickerill and others believe them to be produced by the periodic activity of the enamel cells as indicated above. Von Ebner considers that they are due to the entrance of air into clefts or spaces between the ground-off ends of the prisms. Leon Williams and Hopewell-Smith agree in attributing the striæ to pigmentation.

Other authorities consider that the varying character of the food taken by the mother during gestation, some being rich in lime salts of one kind and some in salts of another kind, is responsible for the striation.



Schreger's Lines in Human Enamel.

Fig. 84.—Markings as viewed by transmuted light. × 40.

Fig. 85.—The higher magnification shows the different directions of the enamel prisms. × 160.

Schreger's Lines.—Other markings run more or less obliquely across the striæ of Retzius, outwards from the surface of the dentine. These are broad shadows or bands called "Schreger's lines," and are an optical effect due to adjacent groups of prisms running in different directions, so that on section some prisms are cut longitudinally and others transversely or obliquely.

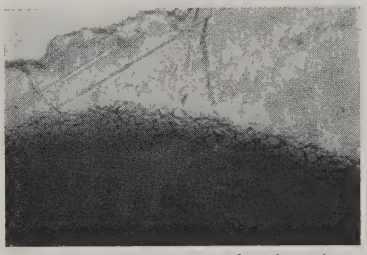


Fig. 86.—Amelo-dentinal junction. Ground section human molar—Silver preparation. × 40.

Amelo-dentinal Junction.—The junction of the dentine and enamel is marked as a thick line, or if the section is not quite vertical, as a broad band between the two tissues, which if critically focussed with a higher power is found to be made up of innumerable convexities with the convex surface towards the dentine. The illustration shows this very distinctly.

Enamel Spindles.—Running from the dentine into the enamel, especially from the point of the dentinal cusp, there are certain irregular spaces projecting some distance into the enamel.

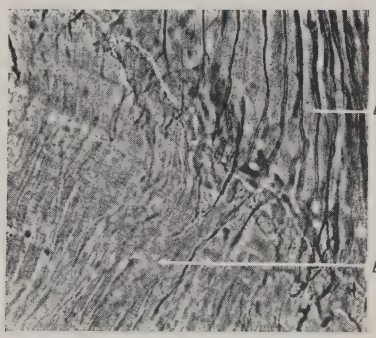


Fig. 87.—Dentinal tubules ending in channels in the enamel. × 160.
D, Dentine ; *E*, Enamel.

The photographs are taken from the point of a premolar cusp (Fig. 88), and from the occlusal surface of a molar (Fig. 89). They may be clubbed or spindle-shaped and are directed mostly at right angles to the dentine surface. They are said to lie in the cement substance which is more abundant at the dentine surface than at the free edge of the enamel. Waldeyer and Hertz deny their existence altogether, while Tomes considers them a pathological manifestation, but their presence is so constant, that one must look upon them as a normal phenomenon like interglobular spaces in dentine. Mummery observes that "it is significant that in those marsupials in which the tube system of the enamel is much reduced, bodies exactly like the spindles in human enamel are found at the amelo-dentinal junction, and also deeper within its substance, and dentinal tubules are often seen passing into these spaces, crossing them and terminating more deeply in the enamel."

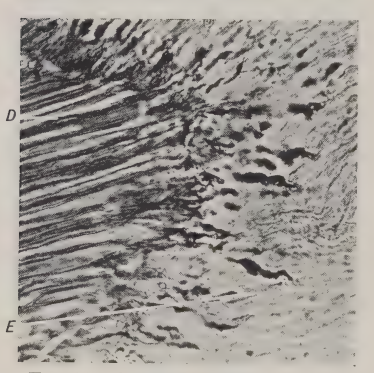


Fig. 88.—Enamel spindles. × 320.
D, Dentine ; *E*, Enamel.

He looks upon them as imperfections in the calcification of the cement substance, and although dentinal tubules may enter them, "they are not dilatations of the tubes, but spaces into which they enter."

Nothing definite is known about the contents of the spindles, which sometimes appear quite black and at others transparently clear. Mummery and others have stained them by forcing dilute fuchsin from the pulp chamber through the dentinal tubules, when they are said to "show a clear uniform coloration."

The theories as to their significance are as follows :—

1. They contain nerve end organs. (Römer.)

2. They are dentinal tubules which have maintained their individuality during the absorption of the first-formed layer of dentine which is said by some authors to occur. (Walkhoff.)

3. They contain protoplasmic masses in direct connection with the dentinal fibrils. (Bödecker.)

4. They are processes of uncalcified dentine matrix thrust into the enamel between the rods.

5. They are hollow spaces produced by the shrivelling up of the cement substance containing air. (Von Ebner.)

Fig. 89.—Enamel spindles with granular contents. × 320.

Fibrous Bundles. — The most striking feature in this section is the large number of markings jutting into the enamel from the amelo-dentinal junction.

These markings start at the dentine margin as a tiny fissure which spreads out into the enamel in a brush-like manner. They are frequently to be seen in vertical sections and are quite distinct from the enamel spindles.

Fischer has figured them, and Mummery has a photograph showing what he calls "fibrous bundles" at the amelo-dentinal junction. This writer points out that imperfections of structure are very common in the enamel near the junction of the two tissues, and obviously considers these bundles to be defects of development.

They often appear to be connected with dentinal tubules entering the enamel, but appearances in such thick sections as ground sections necessarily are, and in the preparation of which it is impossible to be certain that the plane of the horizontal or the vertical is quite accurate, are apt to be very misleading.

It has been suggested that these so-called fibrous bundles contain living protoplasm which, through the dentinal fibrils, is in direct connection with the blood stream, and that they lead to minute channels which everywhere permeate the enamel.

Stains will penetrate the enamel from the pulp chamber via the dentine. This has been shown by Caush, Von Beust, Mummery and others, and it is possible by prolonged treatment of a tooth in bulk with pyridine and nitrate of silver to show penetration of the enamel from its outer and its inner surfaces (Fig. 82). But this is by no means proof of the presence of living organic matter, and prolonged search of a great number of preparations both stained and unstained, has failed to discover the minute channels described by Von Beust.

It is possible that the conception of enamel as a dead inorganic substance quite beyond the effect of fluctuations in bodily condition may have to be modified with increase of knowledge. There is no doubt that the enamel of a tooth that has survived until adult life is harder than that of a newly-erupted tooth. What exactly the hardening process is we do not know, whether it is a physical change comparable to the slow setting of concrete, or whether it is a more intimate union between the calcium salts on the one hand, and the mucinous secretion from the ameloblast, which probably forms the slight organic scaffolding of the tissue on the other, or whether more calcium salts are taken up, are questions which have yet to be solved. Some observers even doubt that change in the enamel takes place at all, but we do not think it can be seriously questioned by experienced clinical observers, and those who have had much experience of decalcifying teeth cannot but have been struck with the difference in the effect of the acid on a young or an old tooth.

Permeability of Enamel.—This must be considered from two points of view—

(*a*) The physiological;

(*b*) The physical.

(*a*) Permeability as used in the physiological sense is concerned with the vital activity of living cells whereby they exercise selective power as to substances which shall pass into the cell to be used, and to those which shall be rejected. The process is ultimately a physico-chemical one, as probably are all vital processes, if we include electrical phenomena amongst the physical, but the essential feature is the power of selection.

This is illustrated in the tooth germ by the difference in the product of the activities of the ameloblasts and the dentine forming cells.

The enamel and dentine differ not only in the degree of hardness and the relative proportions of organic and inorganic constituents, but also in chemico-physical properties. This is shown in the different reactions of the two tissues to staining reagents, and especially such as are introduced into the animal during life. With trypan-blue for instance the formed enamel of a developing tooth takes on a brilliant blue, while the dentine remains almost unstained. It is obvious that if the view of the enamel as a completely calcified, practically inorganic substance, cut off from the influence of living cells, is correct, permeability in this sense is impossible. It would be necessary to establish the existence of living plasm which is part of an active cell. This has not been done up to the present. Dentine, however, by means of its tubules and fibrils is in direct continuity with the circulatory and nervous systems through the odontoblasts and the nerve terminations.

Physiological permeability is possible in tissues such as bone, cementum and dentine, and is shown by the alterations which occur in them with the advance of age.

In dentine arrested caries may be another manifestation. Whether the converse process can take place in dentine, that is to say, whether calcium salts once fixed can be abstracted, by means of the activity of the odontoblasts and other processes it is not possible to say. It is possible in bone, as shown by the disease of osteomalacia in which the lime salts are abstracted leaving the collagenous matrix, and there is

no reason why it should not take place in such a highly vital tissue as dentine proves to be.

(*b*) Physical permeation of the enamel has been shown to occur both from the outer and also from the dentinal surface. The extent of the permeation appears to be in inverse ratio to the perfection of the structure of the tissue. This is well shown in Pickerill's sections of teeth, the enamel of which had been treated with nitrate of silver.

It is possible to demonstrate in the same section permeation from both surfaces of the enamel, by using methods of reduction such as are employed for demonstrating neuro-fibrils by prolonged immersion in a solution of silver nitrate. Fig. 82 shows a section of a tooth treated in this way. It will be seen that the staining is distributed over the prism and cement substance alike. Also that it is much more intense from the dentinal surface.

There is a possibility that the reagents have passed between the dentine and enamel as the whole tooth was immersed in them. But the intense staining of the dentine throughout, and that of the enamel at the apex of the dentine cusp, seem to suggest that the reagents have passed the amelo-dentinal junction from the dentinal surface.

Von Beust and Mummery have shown that enamel can be stained from the pulp chamber by capillary attraction or pressure.

Von Beust agrees with Guido Fischer in describing minute channels running from the dentinal surface, and said by them to contain protoplasm in the living state in direct continuity with the dentinal fibrils. These are the brush-like figures so commonly seen in transverse sections of enamel (see Fig. 83) and are probably merely imperfections in the calcification of the cement substance of a similar nature to the enamel spindles.

If it could be established that Von Beust and Fischer were right in their contentions, the permeability of enamel would take on a different aspect, and the fluctuations in the incidence of dental caries in the individual during life would be more easily understood.

Prisms.—Human enamel is an almost completely inorganic substance built up of minute rods or columns which

radiate outwards from the outer surface of the dentine to the free surface of the tooth. The rods, which have a diameter of from ·005 to ·006 mm. (about the same diameter as that of a red blood corpuscle) are said to be irregularly hexagonal in transverse section, but it is doubtful if this is so in all cases, some appearing rounded in form, others of an irregular outline, and others again hexagonal. The hexagonal form is said to be produced by the lateral pressure of contiguous rods. The outline of the rod itself is wavy and can be demonstrated by suitable reagents such as nitrate of silver or gold chloride.

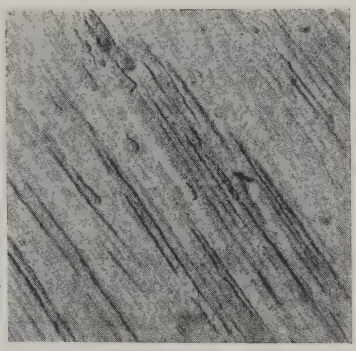


Fig. 90.—Wavy edges of enamel prisms. Ground section of human enamel. Silver preparation. × 160.

The rods are held together by a matrix or cementing substance called the interprismatic cement substance. This appears in sections as minute channels of a material having a slightly different refractive index to the rods.

In a well-calcified section the outlines of the rods and the channels of cementing substance are not easily distinguishable, but the structure can be clearly shown by treatment with dilute hydrochloric or other acid. Such a section or one made from less highly calcified material will demonstrate clearly the structure of the rods and their relationship to the matrix.

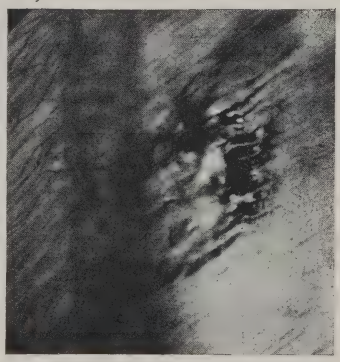


Fig. 91.—Imperfectly calcified enamel prisms showing small globules × 300. Ground section.

It is said that the cement substance varies considerably in amount. According to Hopewell-Smith, "in the majority of cases, in the teeth of man, the rods are more or less in actual contact throughout their entire course, being united by the varicosities or bodies: but in some sections they lie quite apart, separated by matrix

which may equal one-fourth or one-fifth the diameter of a column."

The same author asserts that the cementing material has in it delicate connecting lateral processes and fine tiny granules.

The rods pass outwards roughly at right angles to the surface of the dentine, but it is not possible to follow one from its origin to its outcrop as it does not run far in one plane, being deflected from its original field, and probably at times pursuing a spiral course. In alternate layers the rods are said to run in opposite directions, while sections frequently

Fig. 92.—Enamel of Wart-hog, showing branching of enamel columns. (From Mummery's *Microscopic Anatomy of the Teeth.* Oxford Medical Publications.)

show neighbouring groups of rods cut some transversely, some obliquely, and some longitudinally (Fig. 85).

Supplemental Prisms.—The rods have a slightly tapering end at their dentinal extremity, but otherwise their diameter is approximately the same throughout their course; consequently the greater external area of enamel has to be accounted for either by branching of the rods or by the occurrence of extra prisms. These latter have been called "supplemental prisms," but in human enamel no actual branching rod or "supplemental prism" has yet been demonstrated.

Mummery has shown, however, that in the enamel of Phacochœrus (wart hog) branching rods occur, and between the branches supplementary rods are placed. Pickerill considers that the difference in area covered is made up by the increased width of the rod at the periphery and gives the measurements of 0·0031 to 0·0025 mm. at the dentinal junction and 0·0057 at the periphery. It is not always easy to take measurements at the periphery of the enamel where the rods are comparatively simply arranged, and it is much more difficult at the inner margin, where the conditions are very complex.

Striations.—The individual rods are marked with regular transverse striations which are brought out very distinctly by treating the section with dilute acid for a short time. These markings occur at distances varying, according to Hopewell-Smith, from 3·5 μ to 5 μ apart and coincide on neighbouring rods, so that in a well-marked preparation one gets the appearance of a set of rods running transversely to the original rods. There is some doubt as to the cause of the striations and they have been ascribed to—

Fig. 93.—Striations of enamel prisms. Ground section of human enamel. Silver preparation. × 160.

1. Intermittent calcification.
2. The existence of beads or varicosities in the rods.
3. Unevenness in the surface of the rods.
4. The action of acids,

but there is now a consensus of opinion that they are an effect produced by the globular manner in which the rod is laid down, the point where two globules of calcific matter become fused being the cross striation. The rods are said to be connected to each other by calcified lateral processes, and "calcified plasm strings" running longitudinally through the rod connect the calcified globules or beads of which the rod is built up.

Comparative Microscopic Anatomy of Enamel.—There are many variations in the structure of this tissue as it appears throughout the vertebrate kingdom.

Piscine Enamel.—Tomes states that in the teeth of the Elasmobranch fishes the outermost dental tissue is neither dentine nor enamel, but a compound produced by the activity of epiblastic cells working in a mesoblastic matrix.

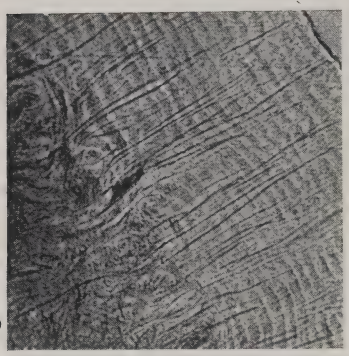


FIG. 94.—Laminated tissue beneath enamel penetrated by dentinal tubules. × 50.

This so-called enamel is often penetrated by a system of tubes which open on the outer surface of the tooth and pass inwards towards the dentine. In many cases there is a double system, one penetrating from without and the other from the dentinal surface, as in the Port Jackson shark (*Cestracion Phillipi*), where the fine ramifications of the dentinal tubules cross into the enamel and mingle with the fine tubes which pass into the enamel from all parts of its external surface at the inner margin of the enamel.

Tubular Enamel in Fishes.—In some sharks the enamel contains lacuna-like spaces which many of the dentinal tubules enter. In the sheep's-head fish (*Sargus Ovis*), tubes pass into the enamel from without at right angles to the surface, and about half-way through its thickness bend right and left, crossing one another, and end at a dark line some distance from the dentine from which it is separated by a narrow clear zone.

FIG. 95.—Tubular enamel of Sargus. Ground section. × 160.

There are no tubules entering the enamel from the dentine.

Other members of the Sparidæ have tubules penetrating the enamel from the dentine in addition to the external system. This is the case in Sargus noctis, a Mediterranean species, and in Sargus vulgaris.

Mummery first described the existence of the two sets of tubules, and concludes that the external tubules are the remains of secreting tubes by means of which the outer portion of the enamel is laid down. More complete tubularization of the enamel is seen in Scarus. The tubes enter from the outer surface, run parallel and straight for about one-third of the thickness of the tissue, and then cross one another and interlace in a most complex manner until near the dentine. No tubules are seen entering from the dentine.

Tubular Enamel in Marsupialia.—In Marsupials, tubules passing from the dentine into the enamel are the normal occurrence, their absence in the wombat providing the exception. Mummery has shown that stain injected into the pulp cavity of a marsupial tooth will pass via the dentinal tubules into the enamel where it penetrates to the extremity of the tubules. The stain also diffuses into the interprismatic cement substance in places; "in fact in many of these sections the enamel appears to be more fully stained than the dentine."

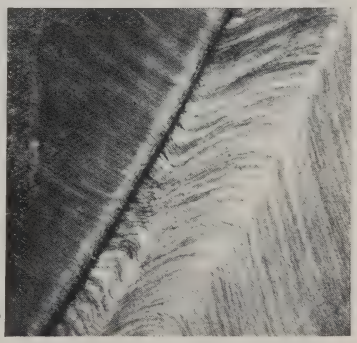


FIG. 96.—Tubular enamel. Kangaroo incisor. Transverse section. × 40.

There is much dispute as to the position the tubules in the enamel occupy in relation to the prisms.

C. S. Tomes and Hopewell-Smith look upon the tubes as the axial portions of the prisms which have failed to calcify. They are in fact true enamel tubes and not dentinal tubes, their connection with the latter being in the nature of a union of two different sets of tubules.

Mummery and others, however, do not agree with this view. They believe the tubes to be prolongations of the dentinal tubes which run in the cement substance between the prisms and not in the body of the prism.

There would appear to be much more organic matter in marsupial enamel than in that of placental mammals. This is shown by the amount and intensity of its staining, and also by the fact that in decalcification experiments its character-

istic form is retained after removal of the lime salts (Mummery).

Tubular Enamel in Mammalia.—Tubular enamel is also found in Hyrax (the Biblical coney), in certain of the Insectivora, in Sorex (the shrew), and amongst rodents in the Jerboa.

In each of these cases the enamel tubules are said to be continuous with the dentinal tubules.

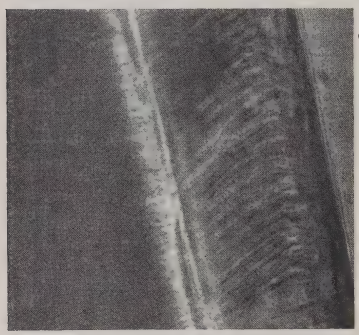


Fig. 97.—Tubular enamel. Tupaia, the Tree Shrew. × 160.

Some degree of penetration of the enamel from the dentine has been described in many carnivora by Tomes, and in the molar tooth of the elephant by Mummery.

It is thought that the presence of tubules in the enamel continued from those of the dentine is a primitive character "to which some slight tendency to revert has not been quite lost by placental mammals" (Tomes).

Enamel of Rodents.—The enamel of the persistently growing incisors of rodents is interesting for three reasons.

(*a*) It is often deeply pigmented (porcupine, beaver, squirrel, rat).

(*b*) It is distributed only on the front and sides of the teeth.

(*c*) Its prisms are so arranged that in the inner portion of the tissue alternating layers decussate, forming a pattern, while in the outer layer they run parallel.

The deep orange pigmentation which is present in some creatures is confined to the outer surface and is said to penetrate some little distance into the enamel substance (Mummery). Hopewell-Smith quoting Tomes states that the colour is in the substance of the enamel itself. In the rat (Mus decumanus) if a sufficiently thin section of an incisor be ground, the pigmentation will appear under a magnification of 50 diameters as a brilliant orange band on the outer surface of the enamel, the remaining portion of the tissue being unaffected by the pigment.

If a tooth be taken from its socket the colour can easily be scraped off the young newly formed enamel; while it floats

off the incisor as a thick membrane if treated for twenty-four hours with 5 per cent. hydrochloric acid.

The enamel being confined to the front and sides of the tooth

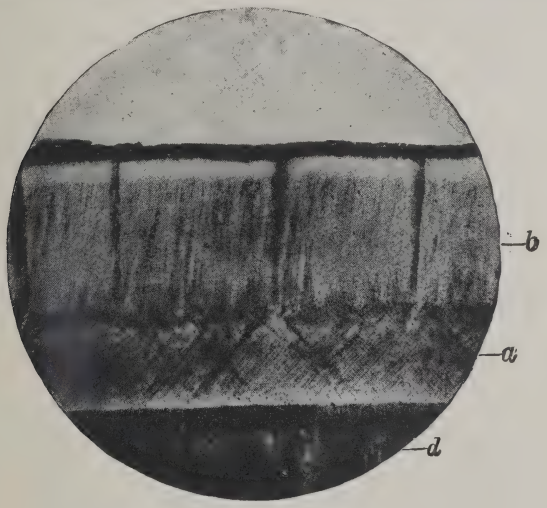


Fig. 98.—Enamel of Beaver. × 225.

d, Dentine; *a*, Inner layer of enamel—decussating layers; *b*, Outer layers of enamel. (From Mummery's *Microscopic Anatomy of the Teeth.* Oxford Medical Publications.)

permits of its unequal wear by means of which the chisel-edge, so necessary for gnawing, is maintained.

The dentine and the cementum which cover the lingual aspect, wearing down much more rapidly than the enamel, leave the latter tissue to form the sharp edge.

There can be no doubt that the arrangement of the prisms is an adaptation to secure the greatest possible strength in the tissue.

Muridæ.—In Mus (the rat), in the inner portion of the tissue there is a decussation of alternate layers which, according to Mummery, forms a diamond-shaped pattern. The prisms are said to be straight, but are sometimes straight and at others curved and are set at an angle of 55° to the dentine surface. In the outer portion they are straight and set at an angle of 25° to the dentine. The edges of the prisms are serrated, the serrations of neighbouring prisms interdigitating (Tomes); but Mummery suggests that the projections are not in the prisms but in the cement substance. The prisms are strongly striated.

Castoridæ.—In Castor (the beaver) the arrangement of the enamel in two distinct layers is very pronounced. Its structure has recently been fully described by Mummery, who points out that the appearances in a transverse section of an incisor are quite different to those in a longitudinal section.

"The inner portion (of a transverse section) which extends not quite half-way across the width of the enamel, is traversed by lines arranged at right angles to one another and making an angle of 45° with the dentine surface. The crossing prisms lie in different laminæ, all those of one lamina passing in the same direction. . . ."

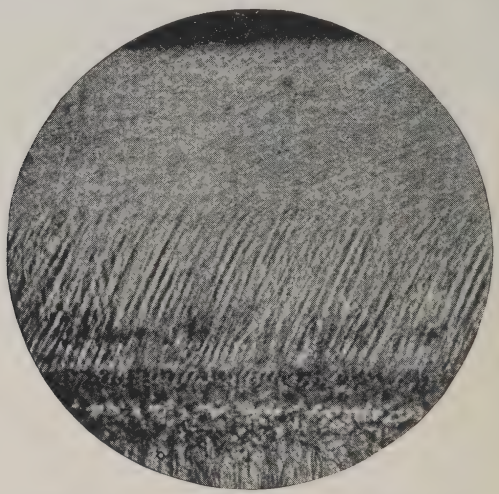


Fig. 99.—Enamel of Castor (the Beaver), longitudinal section. × 250.
(From Mummery's *Microscopic Anatomy of the Teeth.* Oxford Medical Publications.)

In the outer portion the prisms are bent upwards, are parallel and run at an angle of 70° to the dentine surface.

In a longitudinal section the prisms appear parallel in the internal half of the enamel and are set at an angle of 60° to the dentine. In the outer portion the direction of the prisms is abruptly changed to an angle of 30° to the dentine.

Sciuridæ.—The enamel of the incisor of Sciurus (the squirrel) is very thin and its colour is confined to the outer layer. The inner layer, which is two-thirds of the thickness of the tissue, exhibits the crossing laminæ in the transverse section.

The prisms of the outer layer all run in one direction, are slightly curved and are set at an angle of 45° to the crossing

laminæ. There are slight differences in patterns of the prism picture in other members of the family, but Tomes points out that they can be recognized at first sight as belonging to the Sciuridæ.

Hystricidæ.—There are two areas of enamel in Hystrix (the porcupine) as in the preceding families. In the inner area the prisms are flexuous and their courses not in one plane. In the outer area the rods are parallel.

Leporidæ.—In Leporidæ (the hares and rabbits) there are no divisions into inner and outer areas and the prisms are not arranged in alternating laminæ. In the hare the enamel rods are said to be slightly curved and parallel and tubes have been described not continuous with the dentinal tubules.

Fig. 100.—Nasmyth's membrane. Impressions of ends of prism brought out by silver nitrate. × 320.

Nasmyth's Membrane

Nasmyth's membrane is a thin film of varying thickness which is found covering the enamel of the crowns of the deciduous and permanent teeth of man. It is said also to occur in monkeys and sheep.

It can be detached from the surface of the enamel by the action of acids.

It was for long considered to be either the persistent dental capsule or a definite development of a very thin layer of cementum, the survival of the thick layer of cementum covering the enamel of the teeth of ungulates.

This view has lately been restated by Talbot, who looks upon the tissue not exactly as mature cementum, but as an "arrest of development bordering on that tissue."

Recent investigations, however, prove beyond all doubt that it is epithelial in origin.

It consists of two portions :

1. An inner clear layer called the pellicle, which is extremely thin ;

2. An outer cellular layer, which is thicker.

The Pellicle is an exceedingly thin membrane which fits closely over the ends of the enamel prisms. It is so tough and elastic that it is readily distorted in preparing histological sections unless treated throughout by aqueous media. Upon its under surface there are to be found certain markings :

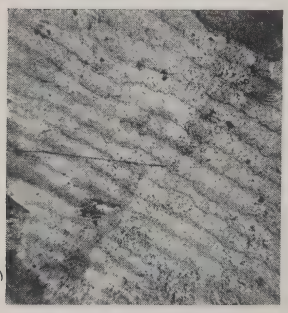


Fig. 101.—Inner surface of pellicle of Nasmyth's membrane, showing parallel markings said to be imbrication lines. × 40.

1. Hexagonal or irregular indentations, impressions made by the ends of the enamel prisms over which the pellicle fits.

2. Sinuous markings or lines more or less parallel which correspond doubtless to the furrows on the surface of enamel described by Pickerill as imbrication lines.

3. On the membrane from unerupted teeth are frequently found attached to the enamel surface a layer of round, oval, or irregularly shaped markings which retain the stain. Where a large number are present they have the appearance of transverse sections of enamel prisms. Their average diameter

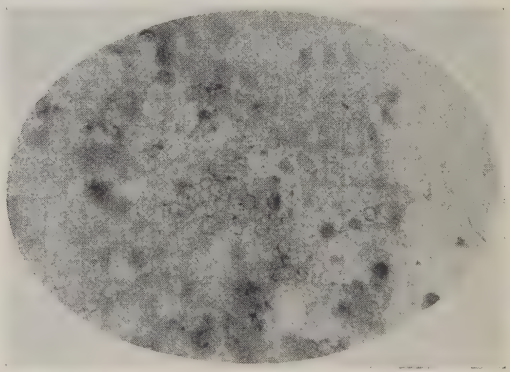


Fig. 102.—Nasmyth's membrane from unerupted premolar, showing round ends of the enamel prisms attached to the pellicle. × 250.

is 0·006 mm., which is comparable to the diameter of the prisms. They are doubtless the ends of prisms which have been pulled away from the surface of the enamel when the membrane was floated off. Amongst these are to be

seen a number of larger deeply staining rounded nuclear-like bodies. Their diameter is 0·007 mm., which is that of the nuclei of the cells to be described. They are doubtless nuclei of spent cells.

The Cellular portion of the membrane consists of one or more layers of flattened polygonal epithelial cells in various stages of degeneration. Well-marked cell bridges such as are seen in stratified epithelia are often to be found.

Mummery figures multi-nucleated cells due to amitotic divisions of the nucleus, a phenomenon which is looked upon

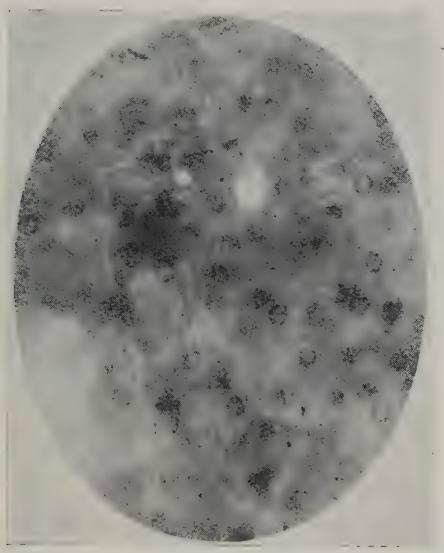


Fig. 103.—Nasmyth's membrane : cellular layer. × 250.

as a sign of degeneration, also cell accumulations and typical cell-nests, other phenomena associated with degenerative changes.

Occasionally one comes across connective tissue cells, and sometimes in the region of a pit or fissure cells similar to bone lacunæ may be present.

The epithelial cells are not all of the same size.

In the specimen illustrated there are principally two varieties, large flattened cells with prominent nuclei, the average diameter of which is 0·025 mm., and smaller polygonal cells which have a diameter of 0·014 mm. Amongst the cells

there are a number of elongated distorted cells to be found of a different character to the rest.

Structure of the Membrane.—The origin of the membrane was stated formerly to be from portions of the enamel organ.

The pellicle from the spent cells of the internal epithelium which had become keratinized.

The cellular layer from the external epithelium.

This view is somewhat modified, however, by Mummery's recent work on the membrane and the tooth follicle, and it must now be accepted that the cellular layer is composed of cells from the internal epithelium, the stratum intermedium, and the external epithelium of the enamel organ; and the

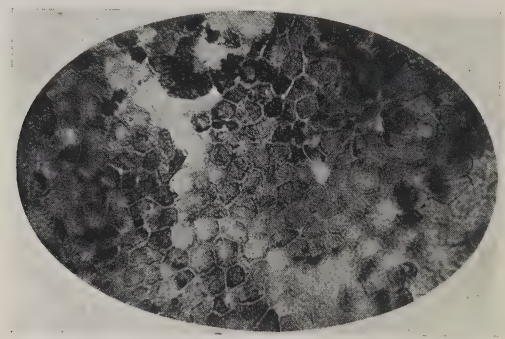


FIG. 104.—Degeneration of cellular layer, either calcification or keratinization. × 150.

cell accumulations and the cell-nests from the epithelium lining the tooth follicle, against which, as the tooth grows, the enamel organ would be squeezed and flattened.

Connective tissue cells and lacunæ-like cells may also be incorporated from the follicle walls.

The clear layer cannot well be the remains of the ameloblasts which have become keratinized, as many of these cells are to be seen amongst the cellular layer and their appearance presents nothing like that found in the pellicle.

One view is that it is a structureless layer formed over the enamel by the enamel cells after their work was completed.

Probably the correct interpretation is that it is the persisting membrane which is said to exist at all stages of formation of the enamel after the commencement of calcification—the

membrana preformativa of Huxley—between the formed enamel and the ameloblasts.

It is generally considered that ultimately the epithelial cells become keratinized and that the membrane is converted into a true horny layer, but no eleidin granules have yet been demonstrated and the appearances of the cells in Fig. 104 suggest that they are undergoing calcareous degeneration.

Functions.—The functions of Nasmyth's membrane are unknown.

The pellicle may act as a dialyzing membrane through which lime salts pass from the circulation to assist in the calcification of enamel as is suggested by Huxley, Leon Williams and Mummery. The theory has been put forward by Pickerill that the membrane acts as an osmotic membrane through which calcium salts in solution in the saliva dialyze and produce a hardening of the enamel after the eruption of the teeth. This is pure speculation and a matter very difficult to establish by experimental evidence.

For it to be at all possible it is necessary to establish the fact that there is living organic matter in the enamel in communication with the body circulation. If this could be definitely proved, the necessity of an osmotic membrane would no longer exist.

CHAPTER VII

DENTINE AND ITS VARIETIES

The tissue which forms the main bulk of the tooth, giving it its characteristic form, and enclosing the tooth-pulp, is **dentine.** Chemically it resembles bone in that it consists of a collagenous matrix impregnated with lime salts, which latter, on being removed by treatment with acids, leave behind a gelatinous substance retaining the form and structure of the original tissue. Histologically, however, dentine and bone have many points of difference.

Varieties.—There are several variations in the structure of this tissue which, adopting Tomes' description, are classified as follows :—

(*a*) Dentines developed on the surface of the pulp, tubules when present radiating from the pulp or its folds.

1. **Ortho-dentine** (hard, unvascular, fine-tubed dentine). This consists of a hard calcified matrix, permeated by a system of fine tubules which radiate from a central pulp cavity to the periphery.

2. **Plici-dentine.**—In this form the tubules radiate from a pulp cavity which has been rendered complex by folding and wrinkling its walls, the tubules radiating from the portion of the pulp to which they belong.

A variety of this is found in some teeth which are made up of a series of denticles, each with its pulp and radiating system of tubules. The tubules of neighbouring denticles anastomose to form the complete tooth.

3. **Vaso-dentine.**—In this variety there is a central pulp chamber and a dentine matrix permeated, not by fine tubules, but by a system of coarse channels which contain capillary vessels in which blood circulates during life.

(*b*) Dentines which are developed by calcification extending through the interior of the pulp.

4. **Osteo or Trabecular Dentine.**—This tissue is most nearly allied to bone. Calcification takes place, not on the surface of the pulp, but within its interior.

The dentinal tubules have relation to the medullary tracts left, and not to a central pulp chamber.

Ortho-dentine

Chemistry of the Matrix.—The organic matrix of this tissue, as of bone and cementum, consists of collagen, the anhydride of gelatin. On boiling in water for some time it is converted into gelatin. The latter when heated to 130° C. gives up its water and becomes collagen according to the following equation :—

$$\underset{\text{(Gelatin)}}{C_{102}H_{151}N_{31}O_{29}} - H_2O = \underset{\text{(Collagen)}}{C_{102}H_{149}N_{31}O_{28}}$$

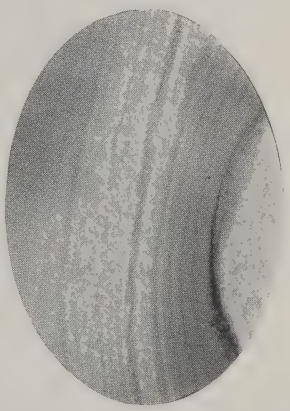


Fig. 105.—Lamination of matrix of human dentine as brought out by the action of the acids of dental caries. Ground section. × 40.

Collagen is dissolved by boiling and by peptic, but not by tryptic, digestion. In addition to the collagen there is a small residuum of elastin left after converting the decalcified matrix into gelatin by boiling. The walls of the tubules are said to be formed of this substance, and it is also said to form the walls of Haversian canals, and of the lacunæ and canaliculi of bone. It is very insoluble except in concentrated nitric or sulphuric acids or hot caustic potash. It differs from keratin in that it contains no sulphur. It is not dissolved by boiling water nor digested by pepsin, but is by trypsin. Analyses of human dentine show that the organic and inorganic constituents occur in the following proportions :—

Organic matter and combined water	20·42 to 28
Inorganic salts	79·58 to 72

The salts chiefly consist of calcium phosphate and carbonate, magnesium phosphate and calcium fluoride.

The salt which is said to be the chief agent in the process of calcification is a double one consisting of three equivalents of calcium phosphate to one of calcium carbonate,

$$Ca_9(PO_4)_6CaCO_3 \text{ or } Ca_{10}(CO_3)(PO_4)_6.$$

The constitution of the dentinal fibrils is unknown. They are said not to consist of albumen.

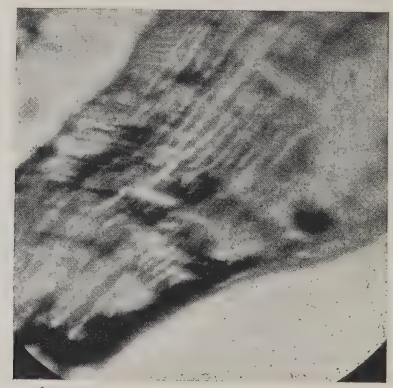


Fig. 106.—Lamination of dentine matrix. Rodent's incisor—decalcified. Silver preparation. × 80.

Structure.—Under normal conditions the matrix appears to be structureless, but under the action of acids a delicate fibrillar basis often appears (Mummery). These fine fibres are derived from the connective tissue of the pulp in which calcification takes place exactly as in bone formation.

Decalcified sections suitably stained often show evidences of the manner in which calcification takes place. The well-marked lamination brought out by the deposition of silver in the accompanying illustration (Fig. 106) of a section of a rodent's developing incisor, suggests the periodic depositions of this tissue just as we find it in bone, enamel and cementum.

There are also certain concentric markings producing a striated appearance in the matrix which, according to Mummery, are calco-globulin contours and mark an earlier stage

of calcification which subsequently becomes masked, giving place to the lamination already described. Near the pulp chamber and bordering the odontoblast cells is a narrow zone

FIG. 107.—Concentric lamination of human dentine—decalcified. Silver preparation.

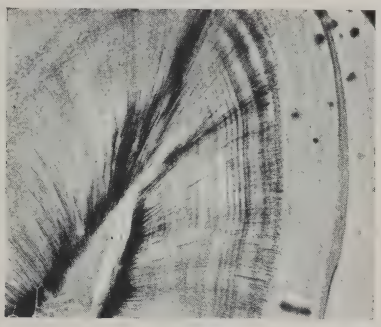


FIG. 108.—Lamination of dentine matrix. Transverse ground section: rodent incisor. × 40.

of lightly staining matrix in decalcified sections which is called the odontogenic zone.

This is the latest formed tissue and in young teeth is not

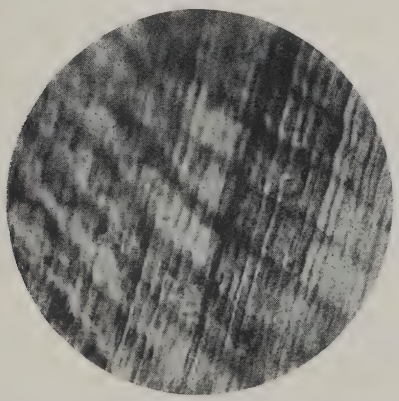


FIG. 109.—Lamination of dentine matrix not due to curvatures of the tubules. Silver preparation. × 300.

yet fully calcified. It exhibits different optical properties to the rest of the matrix, and the fact that it takes the stains less intensely than the more calcified tissue suggests its different chemical or physical constitution.

The Dentinal Tubules.—Everywhere the matrix is

permeated by minute tubes which start by an open circular mouth on the surface of the pulp and radiate outwards gener-

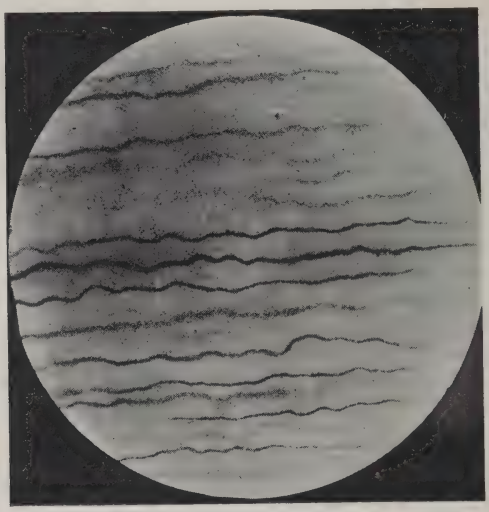


Fig. 110.—Secondary curvatures of the dentinal tubules from the root of a mandibular incisor near the neck of the tooth. Ground section unstained. × 320.

ally at right angles to the pulp surface. At the pulp extremity they are said to have a diameter varying from 0·001 mm., and the distance between neighbouring tubes is said to be twice or thrice the diameter. Their width diminishes gradually towards the periphery. At the amelodentinal junction they frequently end in bulbous enlargements. In their passage from the pulp to the periphery of the dentine the tubules describe a long sweeping double curve somewhat like the letter *f*; this is called the "primary curvature," and is more distinct in the crown of the tooth than in the root. The

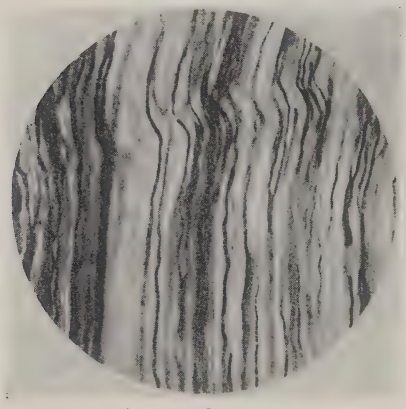


Fig. 111.—Primary and secondary curvatures of the dentinal tubules. The coincidence of the primary curvatures is shown producing the markings known as Schreger's lines. × 300.

course of each tubule is also that of a spiral, so that in addition to the big curve each tube has a series of short waves or twists which frequently disappear from the plane of the section. These short or "secondary curvatures" are more frequently met with in the root than in the crown.

Fig. 112.—Curvatures and dichotomous branching of the dentinal tubules. The branching tubule is seen in the centre of the field—those on the left are not branching. Ground section. × 300.

The tubules frequently branch dichotomously, and also give off tiny anastomotic twigs sometimes at right angles and sometimes at an acute angle to the main tube. The lateral branches are very numerous in the root, but in the crown are found chiefly as the tubule approaches the periphery. They are often to be seen in unstained ground sections, but are best shown by impregnation of either calcified or decalcified material with gold or silver salts.

More thorough impregnation of the dentine of the crown may possibly reveal lateral branches of the tubules throughout their course.

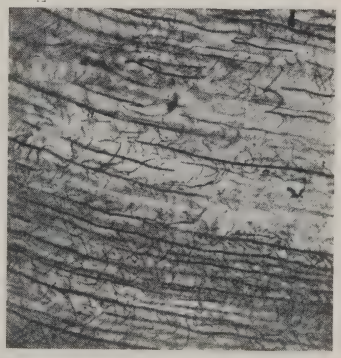


Fig. 113.—Branching dentinal tubules. × 200.

In a transverse section of the dentine a laminated appearance is often seen, the markings of which are parallel with the external surface. These are known as "Schreger's lines" and are due to the coincidence of the primary curvatures of neighbouring tubules. They must not be confused with Schreger's markings in the enamel.

The "contour lines" described by Owen include these and certain markings in the dentine of some cetacea which are due to the presence of rows of interglobular spaces. The tubules

are not of an even diameter throughout, but are subject to slight varicosities. Towards the end of the root, and in dentine at the base of the pulp cavity between a bi- or multiple-rooted tooth, the tubules become very irregular as to course, curvatures, diameter, direction, and branching.

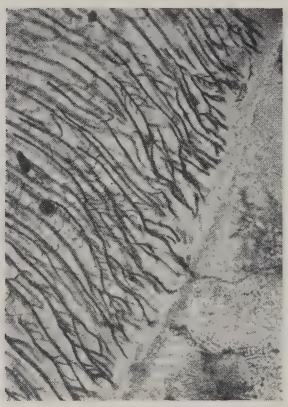


Fig. 114.—Terminations of dentinal tubules near enamel: also shows secondary curvatures of the tubules. × 200.

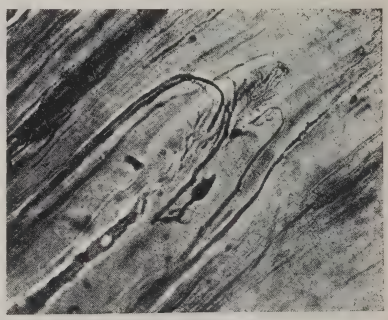


Fig. 115.—Terminations of tubules in root between pulp and cementum. × 200.

Irregular tubules are shown on the floor of a pulp cavity of a molar in Fig. 116, and at the apical foramen of a premolar in Fig. 115.

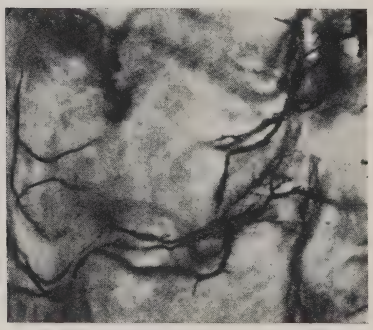


Fig. 116.—Irregular dentinal tubules from floor of pulp cavity of human molar. Transverse ground section. × 320.

The tubules may terminate in one of the following ways:—

1. In branches within the substance of the dentine (Mummery).
2. In peripheral branches which terminate in slightly bulbous extremities.
3. Anastomotic communications with the branches of neighbouring tubules at the periphery or some distance from it.
4. In the spaces of the granular layer of Tomes.
5. In anastomosis with the canaliculi of cementum.
6. In the enamel, either in the spindles or in bulbous

terminations which cross the junction and penetrate some little distance into the enamel.

7. In a pronounced loop.

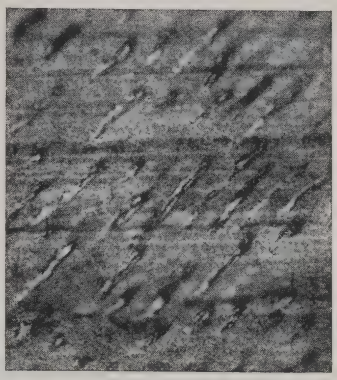


Fig. 117.—Fibrils in dentinal tubules in crown of human incisor. (Preparation made by a modification of Bethe's method for neuro-fibrils.) × 200.

Sheaths of Neumann.—The tubules are said to possses walls or linings which are distinct from the rest of the matrix, and are called the Sheaths of Neumann. That is to say, they are not mere holes or channels in the basis substance, but are tubes which can be demonstrated by histological and chemical methods. After treatment with strong acids or caustic alkalis, or after the destruction of the rest of the matrix by putrefaction the sheaths are still intact and can be demonstrated.

They can be shown *in situ* by Bielschowsky's or Ramon y Cajal's silver nitrate methods, and also by certain aniline dyes in very dilute solutions.

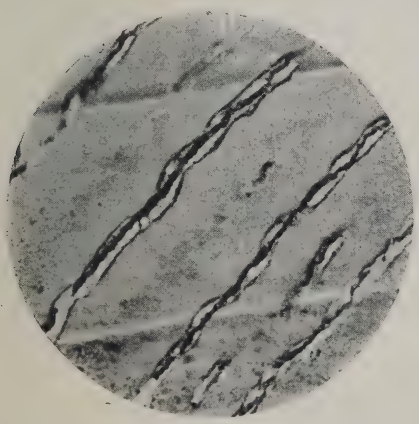


Fig. 118.—Stained dentinal fibrils and walls of the dentinal tubules *in situ*. × 800;

Dentinal Fibrils.—The tubules are traversed by prolongations of the odontoblast cells which are called the dentinal or Tomes' fibrils. In sections with the tooth-pulp *in situ* one can frequently see the fibril stretching across from the odontoblast to the dentine, when the pulp has shrunk or been slightly torn from the dentine wall, as is frequently the case. The fibrils are of some thickness and of firm consistence. They stain with hæmatoxylin, carmine, basic aniline dyes, gold chloride,

nitrate of silver, iron and tannin, etc. They are thought to atrophy in old age. The fibril is said not to fill completely the tubule but to be bathed in an albuminous fluid which everywhere surrounds it. They give off-shoots to the lateral branches of the tubules, the places where they leave the fibril being marked by slight varicosities.

The nature of the dentinal fibril is at present little understood. It is certainly a prolongation of the cell-protoplasm of the odontoblast, but whether it has sensory or trophic functions or both is not even now definitely decided. It is described as a protoplasmic process of an odontoblast cell which is invested in delicate cell membranes, the prolongations of the cell membranes of the odontoblasts (Mummery).

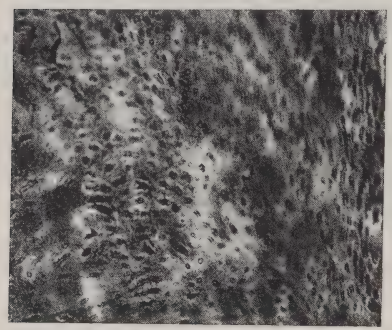


Fig. 119.—Transverse section of dentinal tubules. Silver preparation of decalcified rodent's incisor. × 200.

Hopewell-Smith describes them as "soft structureless threads devoid of a covering of any kind, and continuous through all the length of the tubule and its branches. They are bathed during life with a serous exudation from the surface of the pulp."

Tomes suggests that the fact that they are extensile would indicate their colloidal nature, and he also points out that their outer portion is somewhat firmer in consistency than the interior of the fibril.

There is still much difference of opinion as to the existence of Neumann's sheath, and the relation of the fibril to the sheath or the walls of the dentinal tubules. The most recent work on the subject is that of Hanazawa of Tokyo, who published an exhaustive paper on the subject, *Dental Cosmos*, 1917, Vol. 59, Nos. 2, 3. He says the fibril is a process of the odontoblast and is tubular in form, possessing a bordering layer which is stainable. They are remarkably elastic and pursue a wavy or spiral course in the tubule.

They do not contract by the action of reagents, but on the contrary show a tendency to swell after treatment with acids. The fibril has much more resistance to mechanical and chem-

ical action than the dentine matrix or the wall of the tubule. Its course is marked by nodular swellings, which he looks upon as the points where lateral branches are given off to enter the lateral branches of the tubules, anastomosing with neighbouring branches. There is a space between the fibril and the wall of the tubule in which fluid circulates. This is larger in decalcified sections owing to the contraction of the matrix under the acid.

The wall of the tubule has no special resistance to acids or alkalis. The substance isolated by these reagents is composed of fibrils.

There is no doubt that the fibril is a resilient structure possessing a certain amount of toughness, as is seen in the stretching of the process in sections where the odontoblasts are pulled away from the dentine during manipulation, or where a piece of fibril is broken away from its tubule during manipulation and is found lying across the matrix.

In the section from which the photographs (Figs. 117, 118) were taken many fibrils could be seen cut longitudinally, lying in their tubules, the walls of which are distinctly stained. It will be seen that the fibril does not occupy the whole of the tubule, but is roughly half its diameter in thickness and pursues a more or less wavy course along the lumen of the tube. The rest of the canal is occupied (as is shown in certain parts of the section) by a structureless substance which takes the stain less intensely than the fibril, which appears to be completely surrounded by it. In the recent condition this may be lymph which circulates in the tubules from the pulp, and which has been coagulated by the action of the fixing agent. Here and there one can see minute lateral projections as of branches pulled out of lateral branches of the tubules.

The wavyness of the fibril is not at all unlike that of certain fibres in the pulp which pass up to the under surface of the dentine and which will be described in the section dealing with the pulp.

Mummery describes one or more neuro-fibrils accompanying the dentinal fibril, "which course with it throughout the dentine," but the exact relationship of the neuro-fibril to the dentinal fibril is not yet established.

Interglobular Spaces.—There are certain irregular spaces seen very frequently in poorly formed dentine and often associated with defects in the enamel. They vary greatly in size and shape and their outlines are formed by portions of closely opposed spheres. Globular contours are often seen in the neighbouring dentine. The contents of the spaces may be granular or quite clear, or subsequent calcification may have obliterated them, leaving only their outlines to mark the arrest of calcification. In the dry state the uncalcified matter shrivels up leaving a real space which gets filled with débris in grinding the section.

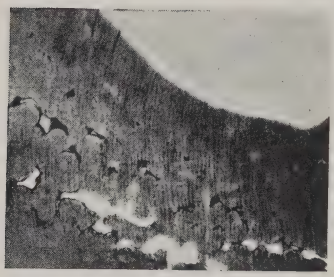


FIG. 120.—Interglobular spaces in dentine. × 80.

The spaces are usually in the crown of the dentine at varying distances beneath the enamel and generally arranged in oblique rows, and in most sections the dentinal tubes cross these spaces without interruption.

FIG. 121.—One interglobular space from the previous illustration showing the outlines of the globular contours. Silver pyridine preparation. × 300.

Granular Layer of Tomes.—In the dentine of the root of the tooth, immediately beneath the cementum, there is seen a band of dark contours which under a low magnification gives an appearance of granularity to the tissue, and so is called the "granular layer of Tomes." The layer, as a rule, is narrowest at the neck and broadest at the apex of the root. It is made up of numberless irregular spaces, some rounded or crescentic in form, others angular. They are much smaller than the interglobular spaces, and, as it is well put by Hope-

well-Smith, "represent a compromise between an interglobular space and a lacuna in hyperplastic cementum."

Near the end of the root, where the spaces are more numerous, they increase in size, and sometimes lacunæ-like spaces with numerous processes may be seen.

FIG. 122.—Granular layer of Tomes in dentine, and cementum lacunæ of deciduous canine. × 40.

Between the granular layer and the cementum there is a clear homogeneous layer and then a dark line, the line of demarcation between the dentine and cementum.

In many instances the dentinal tubules seem to end in the spaces of the granular layer, and processes from the spaces may be seen to communicate with the terminations of the tubules.

The contents of the spaces are said to be protoplasmic in nature and to communicate on the one hand with the dentinal fibrils and on the other with the canaliculi of the cementum, and thus supply a chain of nutrition from the blood vessels of the periodontal membrane to the dentine in case of the loss of the pulp.

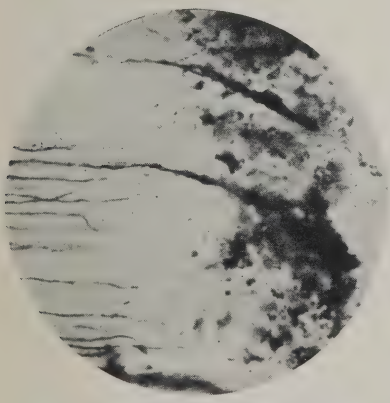


FIG. 123.—Spaces of the granular layer of Tomes with dentinal tubules ending in them. × 400.

Secondary Dentine.—This term is used to describe the tissue that is formed on the surface of the pulp as a protection against injury of that organ, when the tooth is subject to attrition; or the deposition of new dentine which occurs on the pulp surface with advancing age and which may proceed to the complete calcification of the pulp.

A distinction is made by some authors between this secondary tissue and that formed in the pulp in response to the stimulus of erosion and advancing caries. There is, however, no difference in the resulting tissue, and it only leads to confusion of nomenclature to call one "secondary" and the other "adventitious" dentine.

FIG. 124.—Secondary dentine—tubular in character. The outline of the original pulp cavity is well shown, and the continuity of the new tubules with the old. From a tooth worn by attrition. × 37½.

Secondary dentine may be tubular in character, the new tubules joining on to the old.

There is usually nothing to distinguish the new from the original tissue except the outline of the original pulp cavity, and the different direction of the tubules.

In another case the tissue may be more of the nature of that of the granular layer in the dentine of the root.

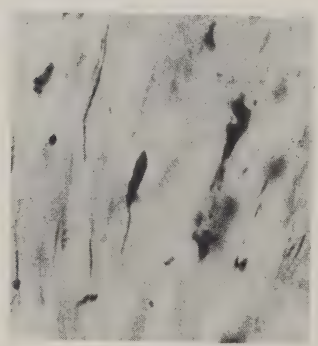


FIG. 125.—Fine tubules ending in oval spaces in secondary dentine from same specimen as Fig. 126. × 300.

FIG. 126.—Tubules ending in irregular spaces in secondary dentine in pulp chamber of a permanent tooth subject to severe attrition. These spaces are not interglobular spaces, but would seem to be analogous to those of the granular layer although much larger. × 300.

Numerous irregular shaped or round or oval spaces may be present in which the tubules end. The tubules themselves are less numerous than in the first variety. Compare the spaces in the illustration with those of the granular layer (Fig. 126).

There does not appear to be any reason why any particular variety of adventitious dentine is formed. The conditions which regulate its deposition are quite unknown.

Plici-Dentine

This form of dentine includes two classes—

(*a*) The dentinal tubules radiate from a pulp chamber made complex by the infoldings of its walls as in Varanus, Lepidosteus, Labyrinthodon.

(*b*) The tissue is composed of separate denticles each with its own pulp and system of tubules which often become fused at their peripheries.

This structure is found in the teeth of early fossil fishes Rhizodus, Edaphodon, and Ptychodus, in fossil batrachians as Labyrinthodon, and in some modern fishes, as Myliobates and Pristis (the saw-fish), in Varanus (the monitor lizard), and in one solitary mammal, Orycteropus (the aardvark).

Fig. 127.—Transverse section: Rostral tooth of Pristis. Plici-dentine. × 40.

In Varanus (monitor lizard) the first formed dentine is orthodentine with a central simple pulp chamber. Soon the edges of the latter become irregular and longitudinal furrows appear on the surface of the dentine. There is, thus, a central pulp with thin radiating processes, each process being responsible for its own system of tubules.

In *Lepidosteus Oxyurus* single columns radiate from a central pulp chamber.

In *Lepidosteus Spatula* the lateral columns are branched and the central pulp cavity is filled up.

In Labyrinthodon extreme complication is obtained by the thin lateral processes of pulp being flexuous. In Myliobates there are short, straight pulp canals in the upper part of the tooth, each canal having its own system of tubules. The terminal branches of one system sometimes inosculate with those of its neighbour.

At the base of the tooth the disposition of the channels is not regular.

The tissue of the rostral teeth of Pristis is similar to that of Myliobates. The columns of pulp vary somewhat in size and

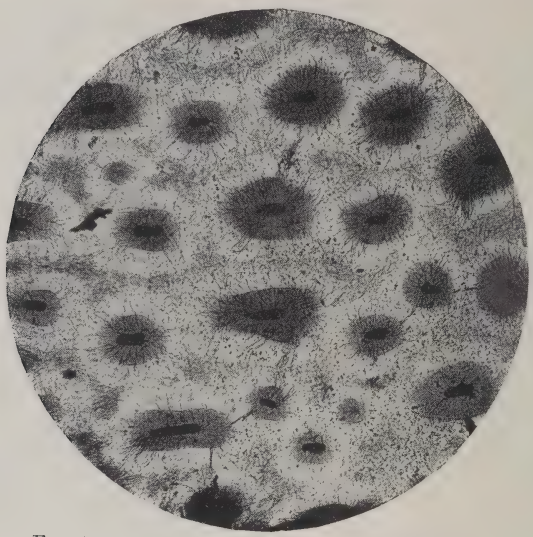


Fig. 128.—Plici-dentine. Rhizodus : a fossil fish.

shape and also in direction, but are usually parallel. They branch dichotomously as they pass towards the point of the tooth. The tubules frequently branch, the branches being as large as the trunk and coming from it at right angles.

Each system of tubes represents a separate denticle, which on transverse section is generally "a more or less regular hexagon." The denticles are fused at their extremities, and the fine terminations of the tubules often anastomose with those of the neighbouring denticle.

In Rhizodus, a fossil fish, which has a structure practically identical with Pristis, the tubules are coarser and less irregular.

In Edaphodon, another fossil fish, the tubes are coarse at first and fairly straight, but in branching become rapidly finer and eventually disappear in fine arborizations, the fine tubes of neighbouring systems anastomosing.

In Orycteropus (the aardvark) is seen the only illustration of a mammal with teeth of a plici-dentine structure.

Vaso-dentine

The fine-tubed system is replaced in this variety by a series of channels much larger than dentinal tubules.

Fig. 129.—Plici-dentine. Edaphodon : a fossil fish.

The channels in the fresh state contain capillary loops in connection with the vessels of the pulp, each canal being quite filled up by a capillary and its blood contents. They are arranged in regular loops, and often, though not always, terminate in a single boundary canal. This is well seen in the hake (*Merlucius vulgaris*).

Fig. 130.—Vaso-dentine. Hinged tooth of Hake. × 50.

Vaso-dentine may pass into tubular dentine at the apex of the tooth, as is seen in Ostracion and Flounder.

The diameter of the canals varies, some being much larger than others, and even in each individual canal the calibre is uneven. Thorn-like processes project into the

matrix and anastomotic loops are seen passing from one canal to another.

Fig. 131.—Vascular channelless dentine of hinged tooth of Hake, decalcified and stained — methyl-blue-eosine. × 320.

The matrix in the hake is apparently structureless except for a longitudinal lamination which is especially seen in the outer clear channelless layer.

Vascular canals are found in the dentine and also in the cementum of the extinct Megatherium, in Manatee, Sargus, Sarcophilus Ursinus (Tasmanian devil), in Cynomys (prairie marmot), and in the dentine of many rodents.

In the Baracuda pike the single row of formidable, pointed, socketed teeth in either jaw are made up of an outer layer of enamel, inside this a clear laminated layer of tubeless dentine, the remainder of the tooth being vaso-dentine.

In the bucco-lingual section the thin outer layer of enamel-like tissue is seen to be beautifully serrated, the serrations being broad and shallow. There is an appearance of a tube system not unlike that of the enamel of Sargus (Fig. 95). The tubeless tissue beneath is very markedly laminated; compare also with the intermediate tissue in the tooth of Sargus (Fig. 94).

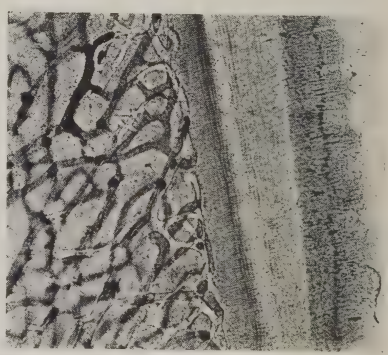


Fig. 132.—Vaso-dentine. Baracuda Pike. Vertical bucco-lingual sections. × 40.

The vascular channels vary considerably in diameter, there are many intercommunicating branches, and the whole system forms a complex entanglement of inosculating canals. In mesio-distal section the serrations on the outer edge of the tooth do not show.

Osteo-Dentine

There is no central pulp cavity in this variety of dentine, the pulp being contained in medullary canals which run longitudinally through the tooth and are continuous at its base with the medullary channels of the bone from which they are often indistinguishable. In the pike there is an outer layer of fine tubes which are collected into coarser tubes, which run into the medullary spaces. The spaces contain pulp "with round osteoblastic cells lining their walls" (Hopewell-Smith).

Fig. 133.—Vaso-dentine. Baracuda Pike. Vertical mesio-distal sections. × 40.

The medullary canals may be mistaken in some instances for the vascular loops of vaso-dentine, but osteo-dentine can be distinguished from the latter—

1. By the absence of a central pulp chamber.
2. The medullary canals are not so regular as those of vaso-dentine and do not form capillary loops.
3. They contain pulp tissue as well as vessels.

In *Carcharias* the crowns of the teeth are of fine-tubed dentine, their bases osteo-dentine, while in *Lamna* the central core of the tooth is osteo-dentine, the outer case being possibly enamel.

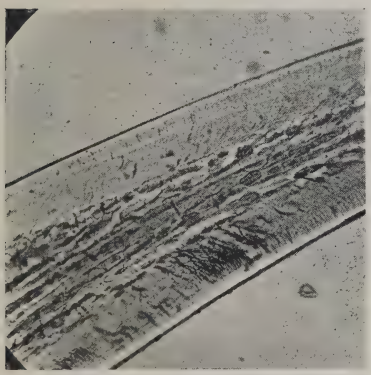


Fig. 134.—Osteo-dentine. Pike. × 40.

In human teeth in old age the pulp is sometimes converted into a form of secondary dentine which resembles osteo-dentine, the normal arrangement of parallel tubes being replaced by an irregular structure through the calcification of the pulp. A similar structure may be seen in the tusk of an elephant when the pulp is injured by gunshot or spear thrust, and in the persistent incisors of rodents when similarly injured.

CHAPTER VIII

THE TOOTH PULP

The central portion of the tooth is in the living state occupied by a soft vascular highly sensitive tissue.

This is the remains of the dentine papilla, the formative organ of the dentine, and is left enclosed in the calcified walls

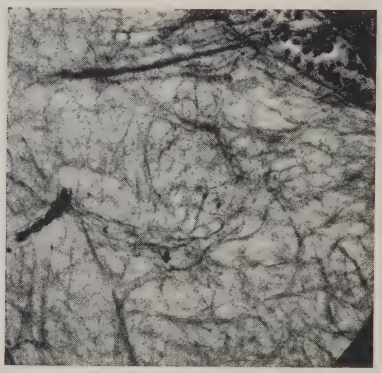


Fig. 135.—Delicate connective-tissue fibres and nerve fibres of the pulp. Cells not stained. × 160.

of the pulp chamber for the purpose of blood and nerve supply to the dentine.

Examined macroscopically after removal from the tooth, it is a soft whitish organ of a peculiar tough consistency, streaked with minute blood vessels.

Connective Tissue.—Microscopically it consists of a matrix or ground substance of connective tissue fibres, the reticulum of which is filled with an albuminoid material in which are found numerous cells, vessels, nerve bundles and fibres, and also a few coarse bundles of white fibrous tissue. The

delicate fibrous basis gives to the tissue a myxomatous appearance not unlike that of Wharton's jelly in the umbilical cord. It is not known whether the fibres are processes of cells or if they arise in the intercellular substance.

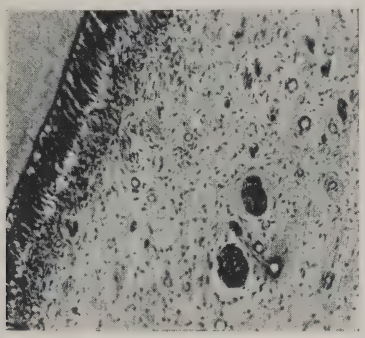


Fig. 136.—Transverse section of pulp of human premolar showing odontogenic zone in dentine, odontoblasts, basal layer of Weil, nuclei of cells in interior of pulp and nerve bundles and vessels cut across. × 50

Mummery considers that they arise apart from the protoplasm of the cells and the accompanying figure seems to support that view (Fig. 135). The fibres are attached to the free

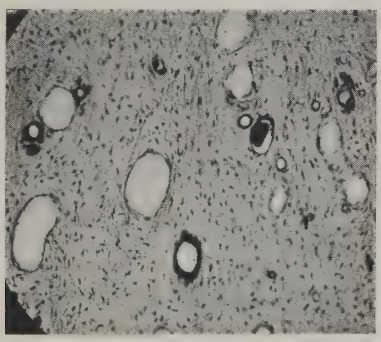


Fig. 137.—Transverse section of pulp of human premolar showing cell nuclei and vessels. × 50.

margin of the dentine in the matrix of which they are incorporated.

Basal Layer of Weil.—Beneath the conspicuous marginal layer or layers of odontoblast cells there is an area said to be

0·025 mm. in width (Hopewell-Smith), which is of a more rarefied substance than the rest of the pulp. This is known as the basal layer of Weil and contains few cells, but is made up of fine fibres, the pulpal processes of the odontoblasts according to Weil. Its origin and purpose and indeed its existence have been the subject of much speculation. It is thought by some to be produced by a shrinkage of the pulp tissue under the action of reagents. Weil, as already mentioned, believed it to be made up of the fine processes of the odontoblasts which in turn were continuous with fine nerve fibres.

Mummery considers it to be entirely occupied by the plexus of Raschkow, and points out that the layer is not seen at the root end of the tooth, where also the plexus is absent. He succeeded in unmounting a section that already showed the layer most distinctly, and subsequently by impregnating the section with gold was able to show the absence of the clear layer, it " being entirely occupied by a dense plexus of delicate nerve fibres." Corkscrew-like fibres first described by Von Korff are seen in developing dentine passing from the pulp across the odontoblasts and entering the dentine (*see* Fig. 72).

Cells of the Pulp.—The appearance of the cellular elements of the pulp varies with the age of the tissue and its period of activity. In the early stage of the tooth germ the dentine papilla consists of closely packed embryonal connective-tissue cells. Soon a special layer of elongated, columnar cells is developed at the periphery of the germ, and persists throughout the life of the pulp, unless affected by pathological conditions. This layer is known as the " membrana eboris " and its cells as " odontoblasts " from the part they are supposed to play in the calcification of dentine.

In the normal healthy adult pulp the other pulp cells are comparatively few and consist for the most part of branching stellate cells whose long branches interlace freely, spindle or fusiform cells and certain round cells of varying size whose functions may be the elaboration of calcific material, the formation of connective tissue fibres, or possibly chemical and nutritional.

Odontoblasts.—The odontoblasts form a single or multiple layer of cells on the surface of the pulp. They commence to differentiate from the other cells of the papilla just prior to the beginning of calcification, and are at first oval, with a large

oval nucleus and little cytoplasm. Then a columnar shape is gradually assumed, and at the period of greatest activity they have been described as "large bipolar, nucleated, epithelioid cells." Their size, which is very variable, is said to bear some relationship to the length of fibril they supply to the dentine, being largest in the coronal portion and shortest in the radicular portion of the tooth. At their period of greatest activity, when they have assumed their maximum size, they attain a length of 50 microns in the ox, and in the adult human tooth they are 25–30 μ in length and 4–5 μ broad. When the dentine is fully formed the cells are reduced in size and become more or less pyriform in the adult pulp, and later are often shrivelled to a "thin fibrous bundle." In the active cell the dentinal end is usually square but may be rounded, the basal end being always rounded.

There is said to be no cell membrane. The cells are slightly separated by intercellular material. The dentinal ends are united by what have been described as "collars," which are not part of the cell itself, but a portion of partially calcified pulp matrix which adheres to the odontoblast. These collars have been wrongly described as lateral processes of the cell.

Processes of the Cell.—Each cell has two sets of processes.

1. That to the dentine—the dentinal.
2. That to the pulp—the central.

The dentinal process enters the dentinal tubule and traverses the dentine as its fibril. A single cell may have from one to six fibrils. The length of the fibril depends upon the thickness of dentine it has to supply and may be as much as 4 or 5 mm. They can be stained with aniline dyes and can be seen stretching across from the dentine to the cell when the latter has been pulled away from the former in the cutting of the section.

The central or pulp process is more difficult to demonstrate: it is exceedingly thin, and passes into the connective tissue of the pulp, but what becomes of it is not known.

The structure of the cytoplasm of the cell is said to be clear and homogeneous in the outer fifth, coarsely granular in the inner four-fifths. The nucleus is large, round or oval, and situated at the pulp extremity.

Blood Vessels.—Branches from the vessels supplying the alveolar process enter the apical region, some going to the

periodontal membrane. One or more trunks enter the apical foramen and passing through the centre of the tissue in company with the nerve trunks branch repeatedly and ultimately form a rich capillary plexus near the surface. Some capillaries may be seen amongst the odontoblasts, and in the developing tooth against the margin of the calcifying tissue. The average diameter of the arteries is about 83 microns, that of the capillaries 8 microns. The nerve trunks are often so closely associated with the arteries that they partially surround them. The veins run with the arteries and can be distinguished from them by their larger size and thinner walls.

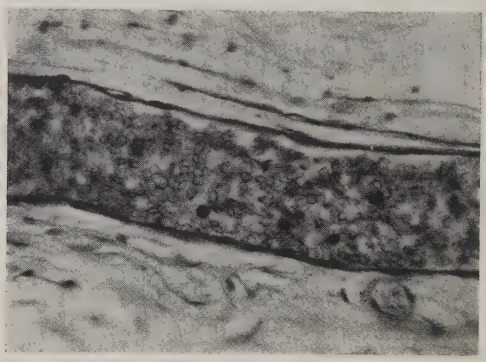


FIG. 138.—Capillary Vessel of Pulp with Blood Cells *in situ*. × about 600.

In structure the walls of the small arteries of the pulp consist of three layers, the *tunica intima*, the *tunica media*, and the *tunica adventitia*.

The inner coat consists of a single layer of flattened nucleated endothelial cells resting on the elastic layer.

The middle coat is the thickest and consists of plain muscle fibres arranged circularly round the inner coat. There is no elastic tissue in this coat.

The outer coat is composed of connective tissue which blends with the connective tissue of the pulp. Sympathetic nerve fibres are said to be present in this coat.

The walls of the veins differ from those of the arteries in that their middle coat is greatly reduced, otherwise they are much alike. They have no valves and are non-collapsible,

being firmly supported by the connective-tissue matrix of the pulp.

The capillaries have walls consisting of a single layer of endothelial cells, linking up the tunica intima of the arteries with that of the veins. The larger capillaries are said to possess the tunica adventitia.

Lymphatics.—It is generally accepted that there are no organized lymph vessels in the pulp. Perivascular lymph spaces are described, especially around the odontoblasts.

Recently, however, Schweitzer claims to have demonstrated the presence of tufts of lymphatic capillaries in the coronal portions which communicate with one or two larger vessels. These pass with the blood-vessels through the apical foramen and "course within the maxillary bone in the upper jaw, emerge through the infra-orbital and other foraminæ into the subcutaneous tissue. In the lower jaw they pass into the inferior dental canal where they run along with the vessels and nerves and thence into the subcutaneous tissue."

The lymphatic glands which drain the gums and teeth are :—

1. The supra-hyoids, lying between the bellies of the digastric muscle, drain the anterior part of the lower gums and teeth, passing the lymph on to the submaxillary group which lie in the digastric triangle on the lower edge of the jaw.

2. The superficial cervical glands which lie along the course of the external jugular vein receive some lymph from the posterior gums.

The deep cervical glands lying along the internal jugular vein receive lymph indirectly from the mouth through the submaxillary glands.

3. The upper gums and teeth drain into the deep facial glands which are placed by the side of the pharynx behind the buccinator muscles. These glands lie behind the tonsil.

Nerves.—The nerve supply for the teeth comes from the second and third divisions of the fifth cranial nerve. The *maxillary nerve* (the second branch) after giving off the spheno-palatine and zygomatic branches, gives off the posterior dental nerve which, entering the posterior dental canal, is distributed to the upper molar teeth and the mucous membrane of the antrum, with small filaments to the gums and cheek. The

middle dental branch supplies the premolars, while the anterior dental branch supplies the canines and incisors, the inferior meatus, and the floor of the nasal fossa.

The third division of the fifth nerve after passing through the foramen ovale is joined by the motor root and divides beneath the external pterygoid muscle into two branches. The smaller anterior branch consists chiefly of motor fibres and supplies the temporal, masseter and external pterygoid muscles, whilst its few sensory fibres are distributed to the buccal mucous membrane.

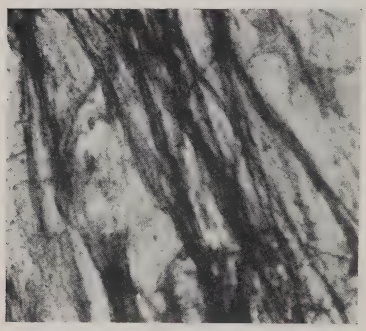


FIG. 139.—Bundles in the pulp in region of neck of tooth.

The larger posterior branch passes beneath the external pterygoid muscle to the outer side of the lingual nerve and enters the inferior dental canal from which it supplies branches to the molars, premolars and canines in the mandible. It then divides into the incisor branch which supplies the lower incisors, and the mental branch which supplies the skin over the lower lip.

FIG. 140.—Nerve bundle from pulp dividing into two subsidiary bundles passing up towards the cornua of the pulp, showing the presence of nucleated and non-nucleated fibres. × 300.

The nerves supplying the pulp pass through the apical foramen with the blood vessels.

At first there are only three or four large bundles of medullated nerve fibres in the lower third of the pulp. Some individual fibres seem to branch off early from the main nerve bundles, and spreading out through the pulp tissue run more or less parallel to the large bundles or pass across from one nerve trunk to unite with another. Others

run to the periphery, and after a course of some distance parallel to the dentinal border beneath the odontoblasts, finally disappear.

The nerve trunks themselves branch dichotomously, so that in the middle third of the pulp there are perhaps eight or nine main bundles, besides smaller ones, and the individual fibres already described.

In the coronal position the main nerve supply appears to be deflected towards the periphery of the pulp.

Fig. 141.—Distribution of vessels and nerves in the crown of a human premolar, Bielschowsky's nitrate of silver process.

The middle section of a series cut vertically from the labial to the lingual surface shows only one or two central bundles running towards the cornua, which soon disappear. At the sides, near the dentine, there are numerous smaller bundles and individual fibres running more or less parallel beneath the odontoblasts, and converging towards the cornua. The bundles soon split up into individual fibres, and there results an almost inextricable confusion of coarse fibres, medullated and non-medullated, which are passing to their ultimate destination, wherever that may be.

Sections towards either side show the nerve bundles becoming more and more numerous until in the extreme sections, the first and last to be cut, the nerve supply is so rich, and the complexity caused by the interlacing of the fibres so great, as to obscure the other pulp structures, and make it extremely difficult, if not impossible, to follow the ramifications of the fibrils to their terminations.

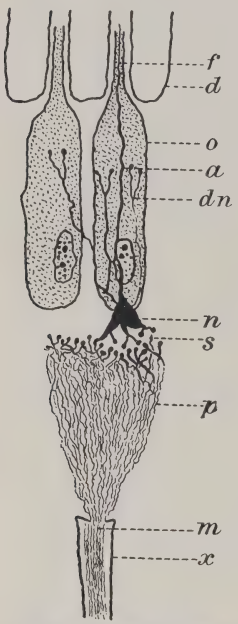


FIG. 142.—Diagram illustrating Mummery's scheme of the distribution of the nerves of the pulp. (Adapted from *The Microscopic Anatomy of the Teeth. Oxford Medical Publications.*)

x, medullated nerve fibre; *m*, axis cylinder of same; *p*, plexus of non-medullated fibres; *s*, synaptic termination; *n*, nerve-end cell; *dn*, dendrons; *a*, axon; *o*, odontoblasts; *d*, dentine; *f*, fibrils.

In premolar sections it is not uncommon to see a nerve bundle pass to the sub-odontoblast region mid-way between the cusps and there split into individual fibres which, bending abruptly to the right and left, run beneath the odontoblasts towards the cornua, where they become lost, as in Fig. 141.

The actual endings of the pulp nerves have long been a source of dispute.

At the present time there are two schools of thought on the subject.

The one limits the nerve distribution to the pulp itself, while the other would trace the nerves to the extremities of the dentinal tubules and even into the enamel and cementum.

Plexus of Raschkow.—There appears to be some confusion as to the *plexus of Raschkow.* Hopewell-Smith writes of "the myelinic fibres which go to form the component parts of the plexus of Raschkow," and shows a photograph of teased out medullated fibres as the plexus.

He repudiates the statement that nerve fibrils enter the dentine and concludes that they "terminate in a basket-work of varicose fibres embracing and often closely attached to the cell walls of the individual odontoblasts."

He thus looks upon the odontoblast as a kind of nerve-end cell and believes that sensation is transmitted via the dentinal fibril. Mummery, however, states that the medullated fibres

lose their medullary sheath, and splitting up into their constituent neurofibrils "enter into a plexus beneath the odontoblast region—the plexus of Raschkow."

The fibrils of the plexus form synaptic connections with nerve-end cells which he claims to have demonstrated existing as a distinct row amongst the odontoblasts near their pulp extremities.

These cells are extremely small, stellate in form, nucleated, and possess two sets of processes. The unbranched distal process, the axon, enters the dentinal tubule with the dentinal fibril, but is not connected with it; and the branching dendrons which form a delicate network around the odontoblasts, and synaptic communications with the fibrils of the plexus, and with the dendrons of neighbouring cells.

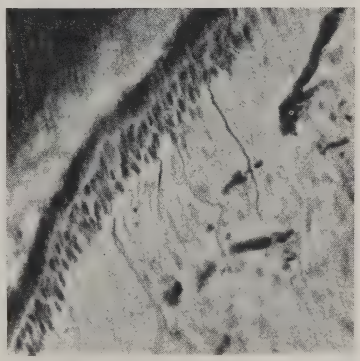


Fig. 143.—Nerve fibres passing to dentine. Decalcified human premolar. Silver preparation. × about 200.

The fibres investing the odontoblasts do not form connections with them. Those passing into the dentine appear as "winding black fibrils within the tubes."

Nodular enlargements are to be seen on them, from which minute branches are supplied to the lateral branches of the tubules. The nerve fibrils traverse the ultimate extremity of the tubules, ending in their terminal arborizations and branches. "Some enter the interprismatic spaces of the enamel and terminate in small bulbous enlargements."

He suggests the possibility of a nerve connection between the dentine and cementum but does not claim to have proved its existence.

Mummery's observations still need confirmation.

The passage of sensory nerve fibrils into the dentinal tubules has been accepted by many of the leading physiologists and anatomists in Britain, and numerous workers have demonstrated fibrils passing across the odontoblast layer to the under surface of the dentine.

Fig. 143 from a silver preparation shows such fibres in their

course to the dentine. These fibres can, in favourable sections, be traced to a nerve bundle. But the interposition of such an arrangement as is described above in the distribution of a sensory nerve is such a radical variation from what occurs

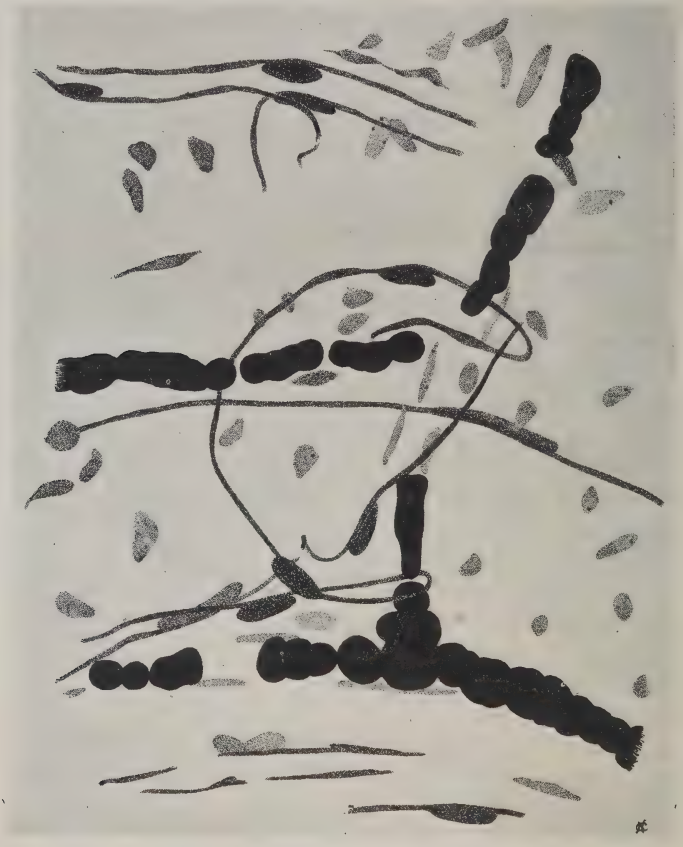


FIG. 144.—Non-medullated unilateral nerve-fibres of the pulp. × 540.

elsewhere in the body, that it can only be accepted with caution.

The majority of the nerve fibres in the tooth pulp are naturally, considering their source, sensory fibres. But one can often see non-medullated nucleated fibres which suggest sympathetic fibres, and Fig. 144 is a drawing of such an one, which is curiously looped around a small blood-vessel. These sympathetic fibres (if they are such) join the fifth nerve from

the superior cervical ganglion of the sympathetic and would accompany the main bundles entering the pulp.

FIG. 145.—Nucleated non-medullated nerve fibres beneath the odontoblasts. × 300.

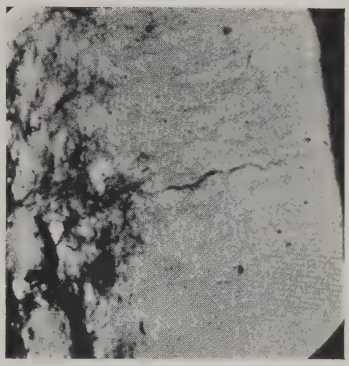


FIG. 146.—Similar to Fig. 147 as if arising from stained masses not unlike those described by Mummery as nerve-end cells. × 300.

Fibres have been described in the pulp as proceeding probably from nerve bundles and passing between the odontoblasts towards the surface of the dentine. These are shown in Fig. 143. They are much coarser than the neuro-fibrils of Mummery, and in certain places appear to possess a lumen as of a sheath.

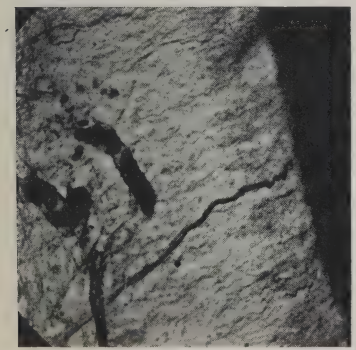


FIG. 147.—Coarse fibril running right up to the dentine which it probably enters although it cannot be demonstrated as the dentine is so black. × 300.

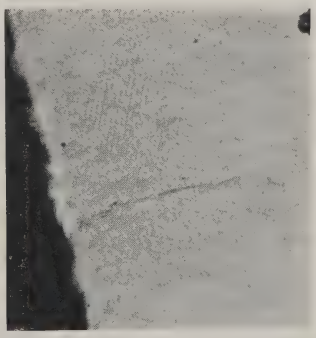


FIG. 148.—Fibril traversing pulp to inner surface of dentine.

It was never possible in this section to establish definitely their connection with nerve bundles, although there could be little doubt as to their nature. Nor could one be quite certain

as to their terminations. All that one could say with certainty was that they disappeared amongst the odontoblasts.

More recent preparations show coarse fibrils running right up to the under surface of the dentine. In character they are not unlike dentinal fibrils. Figs. 146, 147, 148 show the fibrils passing across the odontoblast layer towards the dentine. Note the extreme waviness of the fibril as it approaches the under surface of the dentine.

Careful search disclosed some fibrils more distinct than

FIG. 149.—Fibril branching from main nerve bundle in pulp passing across capillary towards the odontoblasts. × 300.

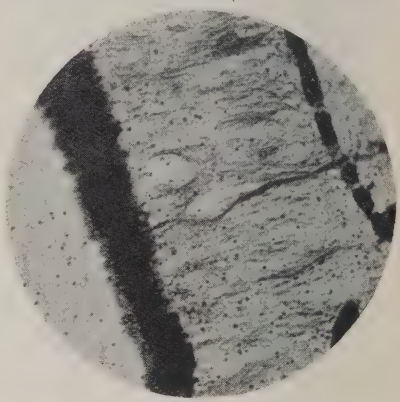


FIG. 150.—The same fibril as in the preceding fig. from the capillary to the under surface of the dentine. × 300.

others which undoubtedly possessed a sheath of some kind with a central more deeply stained axial portion which has all the characteristics of the axis-cylinder of a nerve.

Fig. 151 shows a high magnification of such a fibril with its deeply stained axial portion and its sheath. It is only possible to obtain quite a small area of the fibril in focus at such a magnification on account of its spiral course. Examination of the specimen under the microscope is absolutely convincing.

Again it was not possible for some time to connect the fibrils directly with the nervous system, either through the branching nerve bundles or through a plexus.

Fig. 149, however, shows a single coarse fibril as it branches off from a main nerve bundle and its course towards the dentine up to a capillary just beneath the odontoblast layer; and Fig. 150 the continuation of the same fibril from the capillary to the under surface of the dentine.

It is now therefore definitely established that fairly coarse nerve fibres pass directly from the dividing nerve bundle to the under surface of the dentine. It is not possible to trace them into the dentinal tubules as the margin of the dentine becomes totally black, but their arrangement would suggest

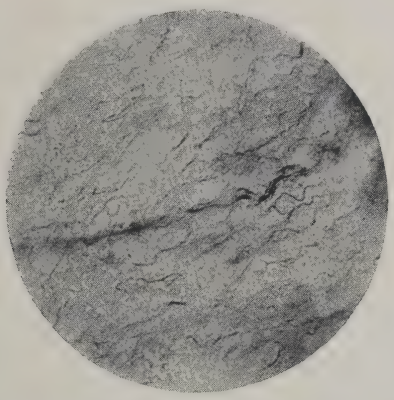


FIG. 151.—Fibril examined under a higher magnification shows a sheath and a deeply-impregnated axis cylinder. × 750.

that their relationship is with the dentine and not with the odontoblasts.

Without further investigation it is impossible to say what is the nature of the sheath. It may be myelinic or on the other hand it may be the neurolemma swollen under the action of the reagents used in preparation.

CHAPTER IX

CEMENTUM, PERIODONTAL MEMBRANE, GUM, THE ABSORBENT ORGAN, AND ALVEOLAR BONE

Cementum

Cementum, the "crusta petrosa" of the older writers, is called "cement" by anatomists, a name adopted by Mummery

Fig. 152.—Relations of enamel and cementum. × 40.

in his recent work; but "cementum" is the term generally used by dental histologists and we have retained the older name.

It forms a thin lining upon the roots of socketed teeth of limited growth. In compound teeth it unites the plates or denticles, as in the elephant, capybara and wart hog. It completely covers the crowns of the teeth of ungulates before they are worn by use.

In structure, chemical composition and development, it is very closely allied to bone, and in thick cementum Haversian canals have been described. It derives its origin from the periodontal membrane, the inner layer of the tooth capsule.

In man, the tissue is thinnest at the neck of the tooth, thickest at the apex, and is more abundant in an adult tooth than on a young root.

The relationship between the cementum and enamel at the neck of a human tooth has been investigated by Choquet who found that the disposition of the two tissues varied considerably, thus :—

The enamel overlaps the cement in a large proportion of young teeth.

In adult teeth, however, the cement overlaps the enamel in the majority of cases.

In a small proportion of adult teeth the two tissues just meet, and in about an equal number there is a slight separation, leaving a narrow strip of dentine at the neck of the tooth unprotected by either enamel or cementum.

Under a low magnification the tissue is seen to be made up of a matrix which has usually a laminated appearance, the

Fig. 153.—Lamination of cementum and Sharpey's fibres. Decalcified human canine. Silver preparation. × 40.

laminæ being marked off by what are known as the "*incremental lines of Salter.*" These are longitudinal markings produced by the periodicity of the deposition of the tissue.

Distributed throughout the matrix in a very irregular fashion are the cement lacunæ which resemble bone lacunæ, and their long branching canaliculi can be plainly seen even with the low power. They are present in the cementum of deciduous as well as permanent teeth, but are frequently absent in young permanent teeth.

Hopewell-Smith, however, considers their presence in human cementum as an evidence of pathological changes. He says : "The cementum of the teeth of man is usually free from lacunæ and canaliculi, being nothing more nor less than a dense, solid, nearly homogeneous band of calcified basis-substance, extend-

ing round the roots." And again, "normal cemental matrix in young and old subjects is therefore nearly structureless. Roots of simple teeth unaffected by morbid processes show this thin layer, which maintains the same degree of thinness throughout its whole extent." This view is also held by Walkhoff.

Mummery and most other histologists consider their presence a normal phenomenon. There are certainly quite a number of cases in which lacunæ are very scarce or entirely absent, from which one may conclude that they are not necessary to

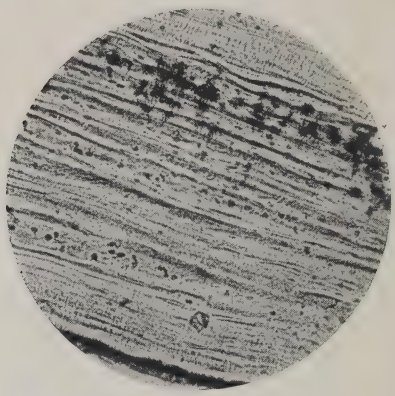


Fig. 154.—Hyperplastic non-lacunated cementum. × 300.

the life of the tissue and therefore when present may be looked upon as accidental.

Fig. 155 shows the presence of a solitary lacuna in what must be regarded as normal cementum, while Fig. 154 in its outer portion shows non-lacunated hyperplastic cementum.

Structure.—The matrix under high magnification is almost structureless or very finely granular. Its relationship to the dentine matrix is so intimate that it is difficult to make out the line of demarcation of the two tissues.

The lamellæ are crossed by fibres analogous to Sharpey's fibres. These are minute rods running obliquely or at right angles across the lamellæ, as if to unite them together, and being continuous with the fibres of the periodontal membrane. It is not known whether or not they are calcified. Tomes considers that they are, but Mummery remarks that

the fact that the micro-organisms in caries of the cementum penetrate these fibres, would suggest that there must be some essential difference between them and the rest of the matrix.

Bundles of these fibres can be demonstrated in the cementum by impregnation with nitrate of silver.

The lacunæ are very like those of bone in their irregular shape, their situation in the direction of the long axis of the lamellæ, and the possession of canaliculi given off at right angles to the lamellæ. It is said that the canaliculi are more numerous on the external side than towards the dentine.

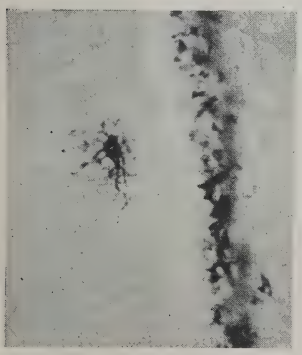


Fig. 155.—Granular layer and cementum from deciduous canine showing solitary lacuna. Compare this and its canaliculi with bone lacunæ, Fig. 157. × 300.

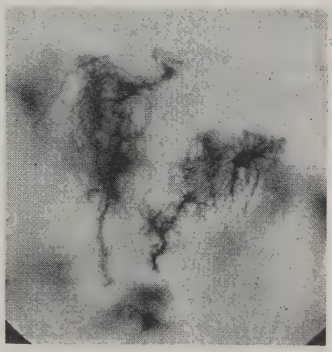


Fig. 156.—Irregular lacunæ and canals in cementum of permanent canine. × 300.

They differ from bone lacunæ in their excessive variability of form and size and in the excessive number and length of their canaliculi.

There is not, however, any essential difference in them.

In the living state each lacuna contains a living cell exactly as in bone, which is called a cementoblast. This cell is said to possess a large, "readily stainable nucleus with one or two nucleoli" (Mummery). The processes of the cell pass into the canaliculi and anastomose with the processes of neighbouring cells, and frequently with the fine terminations of the dentinal tubules in the granular layer, and form a chain of living matter between the periodontal membrane and the pulp.

The Periodontal Membrane

The periodontal membrane, alveolo-dental ligament, root membrane, or dental periosteum, is a connective tissue of considerable density, which occupies the space surrounding the cementum of the root of a tooth, to which it is attached on the one side, on the other being imbedded in the alveolar bone.

Its origin is the outer portion of the tooth follicle.

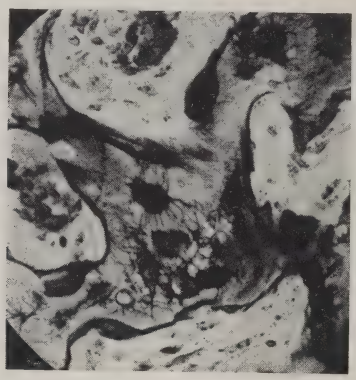


Fig. 157.—Bone lacunæ from developing jaw of a Rat. × 300. Silver preparation. The cells occupying the lacunæ are deeply impregnated with the silver so that all structure is obliterated.

The functions of the membrane are—

1. To act as a means of attachment of the tooth to its bony socket.
2. To act as a cushion to protect the pulp from traumatism following mastication, blows, etc.
3. Nutritive to the cementum and bone of alveolar process.
4. To help in the support of the gingivæ by the arrangement of the fibres at the cervical portion of the membrane.
5. Absorption and deposition of bone and cementum.
6. Tactile function.

To the naked eye it is a dense white membrane. Its thickness varies from 350 to 500 microns and its length from 8 to 20 mm.

It is thickest at the neck and in the apical region, thinnest in the middle of the root; with advancing age the membrane grows thinner and there is naturally a lessened blood supply, which explains the greater susceptibility of the tissue to infective processes with the advance of age.

Fig. 158.—Tooth *in situ* of a Hedgehog showing the arrangement of the fibres of the periodontal membrane—especially the trans-septal fibres passing across from tooth to tooth.

The structural elements consist of fibrous tissue, cells, vessels, nerves; sometimes calcospherites are present.

The Fibres found in the membrane are of two kinds—

(1) The "principal" fibres and

(2) Ordinary connective tissue fibres.

The "principal" fibres are wavy white fibres arranged in coarse strong bands, or loose bundles; which pass across the alveolar space from the cementum to the bone, and are continued in those tissues as Sharpey's fibres.

The arrangement of the fibres varies in different parts of the membrane, and can only be made out in preparations of a tooth in its bony socket with the membrane undisturbed.

At the commencement of the membrane they pass obliquely downwards in the case of the upper jaw, and upwards in the case of the lower jaw, to mingle with the connective tissue stroma of the gingivæ for their support. Following these, the fibres take a horizontal direction, passing over the bony septa to be inserted into the cementum of the neighbouring tooth. These are called the trans-septal fibres. Some of the fibres here pass obliquely rootwards to be inserted into the crest of the bone or periosteum. For a short distance rootwards, the fibres now run horizontally across, but soon acquire an oblique direction crownwards, which they maintain until the apical region is reached. Here they radiate in all directions from the cementum to the bone. Around the apical foramen the fibres are very irregular or almost absent, this area of the tissue being filled with small cells and a few fibres, space being left for the passage of vessels and nerves to the pulp and membrane. According to Hopewell-Smith the apical region may measure 0·5 mm. in width. The function of the horizontal and trans-septal fibres is to support the tooth against lateral displacements and to prevent rotation, while that of the oblique fibres to support the tooth against occlusal impacts. This arrangement allows of a slight amount of upward or downward movement by the stretching of the wavy fibres in the socket, such as one gets in inflammatory conditions. There is also a considerable amount of indefinite connective tissue in the membrane. These fibres are dispersed about the principal fibres, some parallel with the surface of the tooth, others in almost any direction. They are processes of

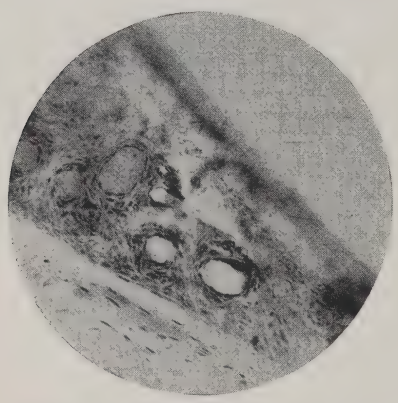


Fig. 159.—Transverse section of periodontal membrane *in situ*, showing fibres, blood-vessels and cells. × 37½.

fusiform connective tissue cells and serve to support the vessels and nerves of the membrane. They fill up all the interstices between the principal fibres.

The Cells of the periodontal membrane consist of those already mentioned, the connective tissue cells, the "fibroblasts" of Black. They are fusiform in shape with oval nuclei, and are drawn out into long branching processes which make a delicate reticulum throughout the tissue.

"Osteoblasts" line the bone of the alveolar process and "Cementoblasts" the cementum.

There is no difference in the appearance of these cells. They are irregularly shaped, with prominent nuclei, and are closely attached to the surfaces of the bone and cementum except where the principal fibres pass into those tissues.

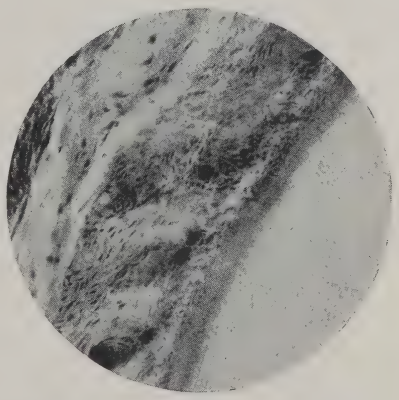


Fig. 160.—Transverse section of periodontal membrane *in situ*, showing cells and fibres. × 37½.

"Osteoclasts" or myeloplaxes are multi-nucleated giant cells which are associated with bone and cementum absorption. They are found in the periodontal membrane wherever absorption is going on, and occupy the bay-like excavations known as Howship's lacunæ.

Clusters of cells which have been described as epithelial cells are seen at a little distance from the cementum. They are looked upon as being remnants of the cells comprising the Sheath of Hertwig. They are rounded or elongated groups of cells not unlike glandular tissue, so that Black was led to describe them as the lymphatics of the periodontal membrane.

Calcified bodies known as "epithelial pearls" are sometimes found in the membrane and are due to the calcification of the epithelial cell remnants.

Calco-spherites are also sometimes to be seen, chiefly in inflammatory conditions.

With the exception of those described by Black, lymphatics have not as yet been found in the periodontal membrane, and those are probably not lymphatics but the remains of epithelial structures.

The Blood-Vessels lie in the central area of the membrane. They enter it from the apical space where they have a common origin with the vessels entering the pulp. They pass down the membrane parallel with the root of the tooth and break up into smaller arteries and capillaries, forming anastomotic communications with the vessels of the gum, the periosteum of the alveolar crest, and the vessels from the Haversian systems in the bone of the tooth socket. Thus a rich collateral circulation is maintained for the periodontal membrane in case the apical vessels are destroyed by suppurative or other processes.

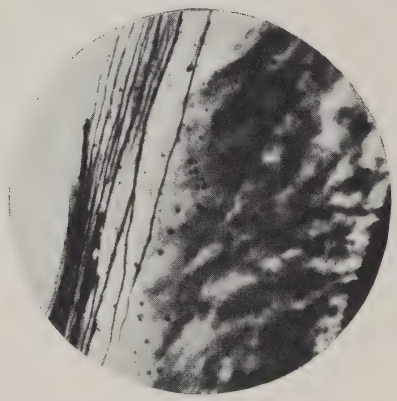


Fig. 161.—Nerve bundle in periodontal membrane. × 300.

The veins accompany the arteries.

The Nerves.—The nerve supply to the periodontal membrane is not very abundant. The nerve bundles follow the course of the main arteries, running parallel with them more or less in the centre of the tissue. The accompanying figure shows a nerve bundle running longitudinally down the centre of the membrane from the nerves of the apical space.

Nothing is known as to their terminations.

A further nerve supply is said to come through the Haversian canals and also over the alveolar border, so that if those from the apical region are destroyed the innervation of the membrane is not seriously interfered with.

"The sense of touch will remain unimpaired, and the sense of pain, in cases of inflammation of the membrane, will be the same as if the periodontal membrane were perfect in all its parts" (Black).

The Gums and Gingivæ

The gum is that part of the muco-periosteum which covers the alveolar processes of the jaws and is continuous with the mucous membrane of the cheeks, lips, floor of the mouth and the hard palate. Those portions of the gum which lie above the crest of the alveolar ridge, and encircle part of the roots and crowns of the teeth, passing between

Fig. 162.—Tooth of rat *in situ*, showing the relation of the gum to the enamel, cementum and periodontal membrane. × 43.

the teeth and uniting with the tissue on the other side, are called the "Gingivæ." There is no difference in the structure of the gums and gingivæ, the latter springing imperceptibly from the former. They have an epithelial covering, which does not differ from that of the rest of the oral cavity, and a sub-epithelial tissue remarkable for the dense fibrous bands which unite with the fibres of the periosteum and bind the tissue firmly down to the bone.

The *epithelium*, which is said to be 0·3 mm. in thickness, covers everywhere the papillæ of the submucous tissue. It is of the stratified type and consists of the stratum corneum, stratum lucidum, stratum granulosum and the rete Malpighii. The flattened cells of the horny layers are being constantly shed, and are found in all the oral secretions.

Cells with well-marked intercellular bridges are common in the deeper layers.

The epithelium is perforated in many places for the passage of numerous mucous ducts from the glands in the sub-mucous tissue.

The sub-mucous tissue is projected into numerous and regular papillæ upon which the cells of the rete mucosa rest. The papillæ may be simple or compound, and can be seen without magnification if the epithelium is removed. The tissue consists of dense bundles of connective tissue fibres which are closely united with the fibres of the periosteum and the "principal" fibres of the periodontal membrane. The fibres pass to the papillæ in "fan-shaped fasciculi."

Plasma cells, mast cells and leucocytes are said to be found among the fibres. Also mucous glands, abundant blood-vessels, few nerve fibres, the glands of Serres, and "lobules of fat cells embedded in a fine reticulum of alveolar tissue" (Hopewell-Smith).

The mucous glands are said by the latter author to be confined to the gum on the palatal side of the teeth, and to be absent from the labial and buccal aspects, a very unlikely condition. The glands of Serres are clusters of epithelium found some little distance from the surface of the gum. They are looked upon as remnants of the tooth band and have no known function. An important rôle has been ascribed to them in the eruption of the temporary teeth (Warwick James).

Black describes the gingivæ as consisting of "the body," "the free gingivæ," and "the septal gingivæ." "The body" is that part which rests upon the alveolar process, and forms a soft extension of that process as far as the cervix of the tooth. The remaining portions of the gingivæ are grown upon the "body." The "free gingivæ" are those portions which embrace the buccal, labial and palatal surfaces of the enamel. The "septal gingivæ" occupy the interproximal space. As they pass towards the occlusal surface the "free gingivæ" thin down to a very thin edge called "the crest of the gingivæ." The space or trough which exists between the "free gingivæ," the "septal gingivæ," and the enamel is called the "sub-gingival space." This is occupied in the healthy mouth

by epithelial and other débris, by bacteria and polymorphonuclear leucocytes which have probably wandered from the blood stream between the epithelial cells ; large endothelial cells may also be present and occasionally the "endamœba gingivalis."

Black describes in the septal gingivæ a lobulated mass of epithelium which has the appearance of a gland, and to which he gives the name of "the septal gland." He does not ascribe any special importance to it. The periodontal space is closed by the epithelium which forms the floor of the sub-gingival space, and which appears to be attached to the cementum, and so long as this is intact and normal, extraneous agencies cannot affect the periodontal membrane.

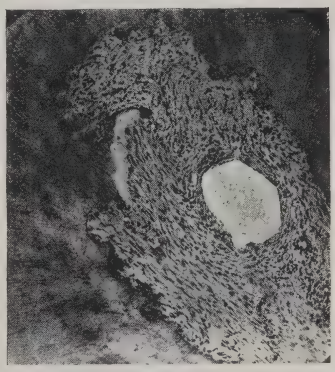


Fig. 163.—Absorption of deciduous molar showing the bay-like recesses and the absorbing tissue *in situ*. (Photomicrograph from a preparation of Mr. Lewin Payne.) × 57.

The Absorbent Organ

The physiological process of absorption of the deciduous teeth results in an excavation of the hard tissues commencing at the cementum, often at some point distant from the erupting permanent tooth, and bag-like depressions are formed, which are known as Howship's lacunæ. The recesses are said to be occupied by large multi-nucleated giant cells, the so-called Osteoclasts.

These cells are looked upon as the active agents in the process ; and it is thought that they work by means of an acid secretion which dissolves out the lime salts, the remainder of the action being phagocytic.

Hopewell-Smith describes the "absorbent organ" as "a thin, white, insensitive organ covering the excavated parts of the roots of deciduous teeth " which is divided from "the outer layer of the dental capsule of the permanent teeth."

It consists of a dense connective tissue stroma in which are found cells and blood-vessels. The cells are of the small round

variety, and occupying the recesses in the excavated area are the osteoclasts.

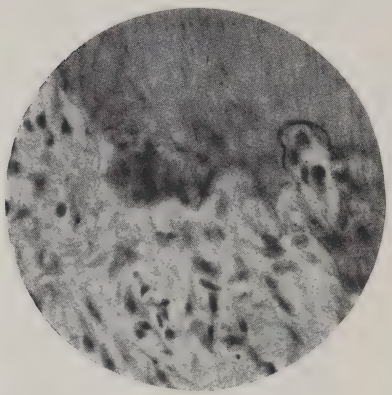


Fig. 164.—Absorption of deciduous molar showing giant cell and Howship's foveolæ. × 300. (Photographed from a specimen kindly lent by Mr. J. Lewin Payne.)

As the pulp is approached, the pulp tissue becomes transformed into the fibrous nature of the absorbent tissue, and the process proceeds from within the pulp chamber as well as from the exterior of the tooth. It is quite common to see in the pulp of a deciduous tooth in which absorption is rapidly progressing, normal healthy pulp in one part, and transformed pulp in another where all the evidences of absorption are clear.

Re-deposition of tissue of an osseous or cemental character is often seen, and in the pulp chamber a dentine matrix is sometimes found filling in the excavated areas. Occasionally one finds cement lacunæ in the newly calcified tissue in the pulp chamber in the physiological process, as well as in pathological absorption.

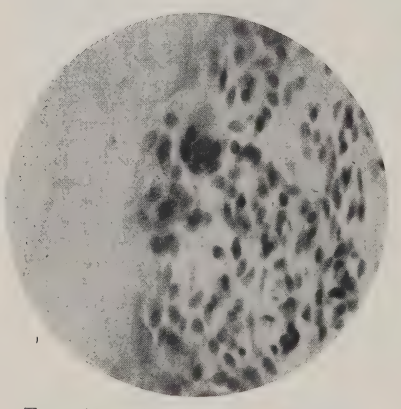


Fig. 165.—Absorption of deciduous molar showing giant cells. (Photomicrograph from a specimen kindly lent by Mr. J. Lewin Payne.) × 300.

Alveolar Bone

The bone forming the sockets of the teeth does not differ from cancellous bone elsewhere having Haversian systems and lacunæ. The cancellous spaces are said to run parallel with the long axes of the teeth. Perforating fibres are well-marked. The external alveolar plate

is considerably thinner than the inner. Between the incisors and canines the bone comes up to a sharp point, and the approximal surfaces are bordered by a sharp well-defined border (the lamina dura) of hard structureless tissue which is clearly seen

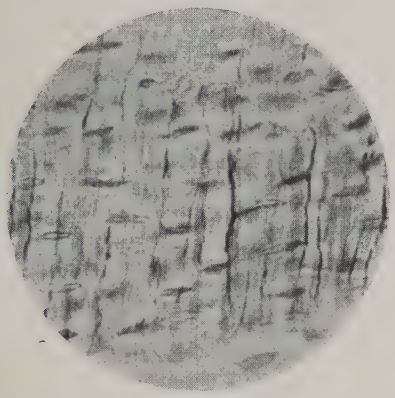


Fig. 166.—Bone of socket of deciduous canine showing perforating fibres. × 300.

in radiographs of teeth *in situ*. The bone does not extend so far in the interdental spaces of the posterior teeth.

The tissue between the two hard plates is of the usual spongy (cancellous) variety.

CHART OF LIFE IN GEOLOGICAL TIME

		Invertebrates.	Fishes.	Amphibians.	Reptiles.	Birds.	Mammals.	Man.
Quaternary or Pleistocene, Recent							Modern Forms	
Tertiary or Cainozoic.	Pliocene . .							Man
	Miocene . .							
	Eocene . .					Modern Types	Placental Mammals	
Secondary or Mesozoic.	Cretaceous or Chalk		Teleosteans Vertebrate Fishes Predatory Sharks	Modern Amphibians		,,		
	Jurassic . .					Toothed Birds		
	Triassic or New Red Sandstone				Primitive Reptiles		Monotremes and Marsupials	
Primary or Palæozoic.	Permian . .							
	Carboniferous Coal Measures		Cestracionts	Amphibians Labyrinthodonts				
	Devonian or Old Red Sandstone		Dipnoi					
	Silurian . .		Ganoids and Elasmobranchs					
	Ordovician .	Shell Fish						
	Cambrian . .	All chief classes of Invertebrates						
Azoic.	Pre-Cambrian or Archæan	Without Life						

PART II

COMPARATIVE DENTAL ANATOMY

CHAPTER X

INTRODUCTION TO COMPARATIVE DENTAL ANATOMY

Zoology, the science of animals, includes and is founded upon a number of daughter sciences.

I. Systematic Zoology, i.e. the classification of animals, the earliest ordered science, was reduced by Cuvier to a system, which is—

1. Based on morphology, not habits or outward appearance. Thus the shark and porpoise resemble each other in habits and appearance, but one is a fish, the other a mammal; the wombat, rat, and cheiromys, existing in widely distributed countries, have a similar dentition, but the first is a marsupial, the second a rodent, and the third a primate. Thus we see three animals, belonging to different orders, in widely separated parts of the world, which by adaptive modification of their teeth have assumed a rodent-like dentition.

2. The animal kingdom is subdivided into sub-kingdoms, classes, orders, families, genera, species, also into numerous and complex classes, sub-classes, sub-orders and groups. Classification is not by numbers, like the corps, divisions, and brigades of an army, but by greatness of divergence in structure. Thus the sub-class of reptiles, rhyncocephalia, contains only one living species, sphenodon, while the single family of squirrels belonging to the order of rodents, contains 12 genera, and upwards of 100 species.

3. Increasing complexity of structure, as the tree of life ascends, suggests evolution from lower to higher forms. The evidence leads to the conclusion that the various forms of life

have descended, or have been evolved, from simpler ancestors, and these from still simpler, and so on back to the mist of life's beginnings.

II. Embryology is the study of the development of animals in which it is shown that an embryo in its various stages represents the progress of its race throughout the ages, and its life seems a reproduction of evolutionary history. In early stages mammals have gill arches like fish; even in the early stage of the human embryo gill slits are present. These embryonic or vestigial structures are common to reptiles, birds, and mammals, and being apparently useless are regarded as traces of ancient history. Gill clefts are still used for respiration in all vertebrates below reptiles.

The fœtal whalebone whale has tooth germs which are never calcified, but though now functionless, owing to the growth of baleen plates in their place, the embryonic teeth survive, and represent structures which once were of active use.

Snakes, though apparently limbless, occasionally retain evidences of rudimentary hind legs, as in the small clawed structures sometimes found in the boas and pythons, suggestive of a period when their ancestors progressed on four legs.

Analogous structures are those with similar functions but of different origin, as the wing of a bird and the wing of an insect, both being organs of flight, but dissimilar in origin; or the teeth of snails and mammals, which serve the same office, but have a different derivation.

Homologous structures are of the same origin—as the wing of a bird, the flipper of a whale, the foreleg of a horse, and the arms of a man, which though dissimilar are modifications of the same limb.

III. Palæontology is the study of extinct life preserved in rocks, as fossils. The geological record is necessarily fragmentary and imperfect; there is no continuous chronicle, for vast periods often separate one geological epoch from another, so that the account is incomplete, and the transition startling. Thus in the Cretaceous and Eocene the forms of life are quite dissimilar, the great reptiles disappearing and mammals taking their place with apparent suddenness. On the whole, reading the register carefully through the various stages of geological

time, in spite of its many imperfections, we can trace the orderly continuity of life, and evolution of forms, resulting ultimately in those which now inhabit the earth.

Professor Ramsay states that the sedimentary rocks in Britain, that is strata formed by the action of water, such as gravels, mud and sand, measure over 72,000 feet, or nearly 14 miles in thickness, and contain, sealed up as in a book, the story of palæontological life.

It is only under peculiar conditions that specimens have been preserved, and the majority are those found embedded in the mud of ancient lakes, or the estuaries of rivers, or in beds of shallow seas.

A body carried into a river would float onwards towards its mouth and would rapidly decay, the various bones fall apart in the journey to the river bar, being distributed over wide areas, so that the chance of finding a perfect skeleton would be relatively small; that is the reason why more numerous fossil mandibles have been discovered than crania with their numerous bones. A body exposed to the air would be speedily destroyed, the flesh by carnivorous animals, or birds of prey, and the bones by disintegration from the acidifying action of carbonic acid in the atmosphere dissolving out the lime salts. Therefore it is not strange that the geological record is incomplete, and that many links are wanting, and that we know so little of the history of the past.

In some of the sedimentary rocks, as the Flysch formation, which consists of shale and sandstone, estimated to be 6,000 feet in thickness and extending for 300 miles from Vienna to Switzerland, Darwin records that "in this vast area no fossils except a few vegetable remains have been found."

It is the same with the English Trias, or New Red Sandstone, over 3,000 feet in thickness, extending over an enormous area, in which hardly any fossils have been discovered; and yet this represents a period of many millions of years, of the life of which we know practically nothing.

Azoic Period.—The earth existed for æons of time before the first evidence of life appeared: the earliest rocks are unfossiliferous. Probably the conditions were such in the slowly cooling globe that existence was then impossible, and the rocks, known as Pre-Cambrian, are described as Azoic, or lifeless.

The fossiliferous rocks are divided into three periods:

Primary or Palæozoic, Secondary or Mesozoic, and Tertiary or Cainozoic.

Palæozoic Period.—*Early Life, Invertebrates.*—It is not until the Cambrian era is reached that definite evidence of life is revealed by the fossil forms of lowly invertebrate creatures: shellfish, trilobites and graptolites. These were the chief denizens of those ancient seas for myriads of years, for as yet fishes were unknown. The chart prepared by the British Museum authorities for their fossil guide-books shows the relative lengths of epochs as represented by the thickness of rocks. It will be seen that for more than half geological time there is no sign of higher forms having existed, either on the land or in the seas.

Appearance of Fishes.—Towards the end of the Silurian a momentous change in the order of life was ushered in by the appearance of small, archaic-looking fishes whose fossil remains have been discovered in Upper Silurian rocks near Ludlow, and in strata of the same age in Lanarkshire.

The fish bed near Ludlow, only a few inches in thickness, is a mass of small spines, which covered the skin, as in the shagreen of the dog-fishes of the present.

It was an epoch-making period, denoting the dawn of vertebrate life, the threshold was crossed and the foundation of the new order established, leading up to the reign of backboned creatures, which in orderly sequence progressed from the cartilaginous fishes to amphibians, reptiles, mammals, and finally to humanity.

In the majority of instances the bodies of the former inhabitants of the earth have entirely perished; but the teeth being formed of hard, and practically indestructible materials, have been preserved as fossils through successive geological epochs, telling the story of the life of the past, and recording the changes in food and environment. The constant modification in the forms of teeth equipped the creatures for the ever-changing conditions in their struggle for existence. No part of the body has been more profoundly altered, and subjected to greater variation, than the teeth, and this in turn has led to the remodelling of the body of the animal, as is seen in the evolution of the elephant, which from a small pig-like ancestor has been completely changed by the modification and lengthening of its incisor teeth.

Devonian Fishes.—The primitive Silurian fishes were succeeded in the Devonian period by grotesque forms, as if Nature were trying her prentice hand. Their bodies were enveloped by enamelled bony plates, and bore some resemblance to a turtle, or were surrounded by scutes ; these were typical fish forms in this age. Their skeleton was cartilaginous, as in the modern sturgeon, and they are regarded as primitive ganoids.

This was the dawn period of the Dipnoi, or mud fishes, possessed of lungs and gills, of which the Lepidosiren of Africa, and the Ceratodus of Australia, are modern representatives.

Carboniferous Fishes.—The Carboniferous, the next period, during which our coal measures were formed, is remarkable for the evidence of the immense numbers of various fishes which then inhabited the neighbouring seas. Great varieties of their teeth are found in the Carboniferous limestone, showing the existence of large ganoids, whose bodies were covered with hard enamelled scales, and resembling the modern American bony pike (Lepidosteus) ; many were probably larger than any existing vertebrate fish, judging by the size of Rhizodus and Megalichthys. In this period also primitive sharks appeared, Cestracionts, of which an example still remains in the Australian seas in the Port Jackson shark (*Cestracion philippi*), a small shell crushing shark, representing a type which has persisted through the Jurassic period to the present time.

Amphibians.—The Carboniferous period gave origin to the first air breathers on land in the form of primitive Amphibians, Salamanders, and Labyrinthodonts, which inhabited the swamps and forests while the coal measures were being laid down. Some of them were of gigantic size, judging by the fossil impressions of their feet in the soft mud. The modern toads and frogs are their puny representatives.

Mesozoic Period.—The Mesozoic period was essentially the Age of the Great Reptiles.

Reptiles.—In the Permian age the first true land reptiles came into existence, and they persisted through the Trias, Jurassic and Cretaceous epochs as the dominant form of life, differentiating into various forms, many of gigantic size, which inhabited the land, the air, the seas, lakes, and rivers, being of insectivorous, herbivorous, and carnivorous habits, like the mammals who succeeded them.

Cretaceous Fishes.—The predatory sharks first appeared in the Cretaceous epoch. Lastly, in the same age the true backboned fishes, with osseous skeletons and soft scales, came into being, and are the precursors of modern fishes.

Dawn of Mammals.—In Triassic rocks are the first indications of lowly mammals, considered to be related to. the monotremes, or egg-laying mammals of Australia, of which the Platypus is a well-known example, a creature which possesses reptilian and mammalian characteristics. Marsupial remains in the shape of numerous small mandibles have been found in Jurassic rocks in England and America, a further step upwards in the evolutionary scale, and the same age gave origin to birds, such as the archaic Archæopteryx, which were succeeded by toothed birds in the Chalk period.

Cainozoic Period.—The Tertiary or Cainozoic period ushered in a new order of life. The great reptiles had disappeared from the face of the earth, apparently with startling suddenness, and the Eocene, or Dawn, introduces us to the age of mammals or warm-blooded creatures, ancestors of the mammalian life of the present, which ultimately culminated in humanity. It was short in comparison with the lengths of the epochs preceding it, but pregnant with possibilities, which have proved of momentous consequence in the history of the world. The reptiles which preceded them had attained to leviathan proportions, and were the biggest animals which have ever trod the earth, but though monstrous in body, the brain was infinitesimal. The Brontosaurus, 80 feet in length, had brains about the size of a walnut ; the reptiles gave place to successors with bigger brains and more specialized bodies.

In many instances sufficient evidence has been brought to light to show the gradual change which has taken place in bodies and teeth from the simple forms of Eocene mammals to the complex and specialized forms of their modern descendants.

Thus Palæontology demonstrates the orderly succession of creatures from the simpler to the more highly differentiated, throughout geological time, succeeding one another in the following order : Invertebrates, Ganoid Fishes, Dipnoi, Amphibians, Reptiles, Primitive Mammals, Birds, Teleostean Fishes, Placental Mammals.

It is by the accumulation of testimony and facts brought together from all parts of the world that we are enabled to grasp the significance of the doctrine taught by Charles Darwin in the middle of last century, and reduce to order the otherwise chaotic observations of past and present life.

The key to the riddle was Evolution, and in the *Origin of Species*, published in 1859, Darwin advanced the theory that species originated by development from earlier forms, and not by special creation, and that by continuous though slow differentiation, creatures ascended from simplicity to complexity. All study of Zoology confirms the correctness of his theory, and points to Evolution as the clue to the problem of life.

By its use we can understand that forms apparently so diverse in structure as the pig, elephant, tapir, horse and rhinoceros were probably all descended from a common ancestor. We are able to appreciate the fact that slight changes in environment and food have produced from Mœritherium, a pig-like ancestor, the stately elephant; and to understand how the gradual lengthening and modification of the incisor teeth in time brought into being the great tusks and developed the tapir-like snout into the modern nervous prehensile trunk.

The descent and evolution of the horse can be traced from Eohippus, a primitive five-toed ancestor, through the ages of Tertiary time, showing the gradual suppression of the toes, until only the one highly specialized toe remains, together with the complete change in the teeth from a brachyodont to a hypsodont dentition.

IV. Artificial Selection.—What Nature has accomplished during the ages man has effected in a comparatively short time by artificial selection, as in the Pekinese dog and the greyhound, descended from common ancestors; the carrier and fantail pigeons produced by selection from the rock dove (*Columba livia*), or the infinite variety of flowers resulting from careful blending of selected individuals of the same species, as in the crossing of the daffodil and narcissus, and from which over a thousand varieties of flowers have been created.

Thus all study of Zoology points to evolution as the key to its problems. The three main factors in bringing about evolutionary changes are—

A. Natural Selection.—Many more creatures are born than can possibly survive, thus excess of offspring leads to struggle for existence, and to the survival of the fittest, that is, those best adapted to their environment ; so that individuals having any advantage, however slight, would have the best chance of surviving, and procreating their kind, while others less provided would tend to decrease and finally to become exterminated.

The beneficial characters would be retained and developed. As Darwin shows, the advantages may be apparently of a slight character ; in the case of the plum with a smooth skin the fruit suffers far more from certain diseases than the plum covered with down, and that purple plums are similarly liable to diseases from which the yellow plum is immune. The constant stimulus to new features produces new species by—

(*a*) The endeavour to exploit fresh possibilities in environment, e.g., land reptiles appear with the development of lungs, birds with development of flight.

(*b*) Changes in environment, such changes being chiefly—

1. Inanimate environment, e.g., climate, food supply ; hence restriction of species in time and space, e.g., the extinction of great reptiles at the close of the Secondary period.

2. More active competitors or dangerous enemies, e.g., the appearance of the great carnivora drives lemuroids south, and leads to the speed of antelopes ; while marsupials, protected in Australia, still survive.

3. Disease : evolution of natural immunity to disease, as in measles and scarlet fever, which are now no longer the dreaded scourges of the past.

Side by side with the development of new useful features are the disappearance of old useless ones, as the rudimentary teeth of whalebone whales, and limbs of snakes.

B. **Sexual Selection** acts by (*a*) Sexual weapons, e.g., tusks of boar, monkey, narwal, horns of rams, antlers of stags, spur of cock. The males armed with the most powerful tusks or largest antlers would stand the best chance in capturing the females.

(*b*) Appearance in courtship, e.g., colours of cock birds, those most gaudily attired, as the cocks of birds of paradise, or the argus pheasant, which display their plumage at the

time of pairing, would compete successfully with less attractive rivals.

C. **Concomitant Variation.**—The males of deer and oxen are usually provided with sexual weapons. Cuvier has stated that if horns or antlers are present, canines specialized as weapons are absent. In the hornless musk deer (*Moschus moschiferus*) canine teeth of great length are produced as sexual weapons, and in the male muntjac canines are present with short antlers.

Odontology is the study of teeth, a very important branch of biology, as the existence of the animal depends upon its teeth, for seizing and crushing the food which supplies it with nourishment.

At the entrance to the alimentary canals of most vertebrates are to be found certain hard substances, known as teeth, which are used primarily for the—

1. Prehension and comminution of food, i.e. as organs of nutrition, and are likewise modified for—

2. Weapons of offence, as the tusks of the boar and narwal and fang of the snake.

3. Locomotion, as in the walrus, where the large canine tusks assist the creature's progress on the ice in the Arctic Seas.

4. Transport, as in the beaver, where the incisors carry materials to build the dams.

5. Tools, as in rodents, for example the squirrel, whose chisel-like incisors excavate the shells of nuts.

6. Protection, as in the tusks of the elephant.

7. Speech, as in man, where the teeth assist in articulation.

Teeth have an infinite variety of forms, from the simple cone of the fish to the complex structure and diverse shapes seen in mammals. These will be studied in the following pages.

A glossary, giving the meaning of the scientific terms used in the succeeding pages, will be found on page 311.

CHART OF THE ANIMAL KINGDOM

SUB-KINGDOM I

PROTOZOA—Single-celled animals. Ex. Amœba.
Chalk-forming Foraminifera.

INVERTEBRATES

1. **Porifera** . . . . . Ex. Sponges.
2. **Cœlenterata** . . . . . Ex. Hydra, jelly-fish, sea anemones.
3. **Vermes** . . . . . Ex. Unsegmented and segmented worms.
4. **Echinoderma** . . . . . Ex. Starfish, sea urchins.
5. **Arthropoda**—
   - (*a*) CRUSTACEA . . . . Ex. Barnacles, shrimps, lobsters.
   - (*b*) MYRIAPODA . . . . Ex. Centipedes.
   - (*c*) INSECTA . . . . Ex. Beetles, moths, bees, flies.
   - (*d*) ARACHNOIDEA . . . Ex. Spiders, scorpions.
6. **Mollusca** . . . . . Ex. Cuttlefish, snails, bivalves.

SUB-KINGDOM II

VERTEBRATES

1. ACRANIA (without skulls) . . . . Three small classes transitional to true vertebrates.
2. CRANIA (with skulls).

Classes.

I **Cyclostomata** . . . . . Ex. Lamprey and myxine. (no jaws, round sucking mouths, horny teeth).

II **Pisces.**
   Sub-classes.
   - A. ELASMOBRANCHII . . Ex. Shark, dog-fish, skate. (cartilaginous fish).
   - B. GANOIDEI . . . Ex. Sturgeon, lepidosteus. (armoured fish).
   - C. TELEOSTEI . . . Ex. All the common species. (bony fish).
   - D. DIPNOI . . . . Ex. Ceratodus, lepidosiren. (double breathers, lungs and gills).

III **Amphibia.**
   Orders.
   - A. *Labyrinthodontia* . . Extinct forms.
   - B. *Caudata* . . . . Ex. Newts, salamanders.
   - C. *Ecaudata* . . . Ex. Frogs, toads.

IV **Reptilia.**
   Sub-Classes.
   - A. CHELONIA . . . Ex. Tortoises and turtles.
   - B. CROCODILIA . . . Ex. Crocodiles.
   - C. LACERTILIA . . . Ex. Lizards.
   - D. RHYNCHOCEPHALIA . . Ex. Sphenodon.
   - E. OPHIDIA . . . Ex. Snakes.
   - F. EXTINCT FORMS . . Ex. Inguanodon, dinosaurs, anomodontia.

V **Aves.**

VI **Mammalia.**
   Sub-Classes.
   - A. PROTOTHERIA, or MONOTREMES . . Ex. Platypus, echidna.
   - B. METATHERIA, or MARSUPIALS.

   Orders.
   - 1. *Polyprotodontia* . . Ex. Opossums.
   - 2. *Diprotodontia* . . . Ex. Kangaroos.

   C. EUTHERIA.

   Orders.
   - 1. *Edentata* . . . Ex. Sloths, ant-eaters.
   - 2. *Cetacea* . . . . Ex. Whales.
   - 3. *Sirenia* . . . . Ex. Dugong, manatee.
   - 4. *Ungulata* . . . Ex. Pigs, deer, horses, elephants.
   - 5. *Rodentia* . . . Ex. Rabbits, rats.
   - 6. *Carnivora* . . . Ex. Dogs, cats, bears, seals.
   - 7. *Insectivora* . . . Ex. Hedgehogs, moles.
   - 8. *Chiroptera* . . . Ex. Bats.
   - 9. *Primates* . . . Ex. Lemurs, monkeys, man.

Further classification of the orders of MAMMALIA is given in the chapters that deal with them.

CHAPTER XI

TEETH OF INVERTEBRATES AND FISHES

Teeth of Invertebrates

It is evident that all creatures require some mechanism by which they can cut and tear their food, and in the lower invertebrates are examples of such appliances.

In the leech are three semi-circular chitinous tooth plates, each armed with from 60 to 100 tiny teeth, and when the creature has attached itself by its circular mouth, the tooth plates come into action like a circular saw, and speedily produce a triangular wound.

The sea urchin (*Echinus*) possesses five large calcified teeth whose tips project in front of the mouth, where they seize and crush small particles of food ; together they form an apparatus known as Aristotle's Lantern, "a complex masticating apparatus."

In the cockroach the powerful jaws are serrated into horny teeth for tearing its food.

Though analogous with the teeth of vertebrates, performing the same functions, the teeth of invertebrates are not homologous.

The mouths of many of the *Mollusca*, e.g. snails and limpets, are furnished with a ribbon-like structure, termed radula, covered with immense numbers of minute horny teeth symmetrically arranged ; this acts as a flexible rasp or file, in the tearing and trituration of food, as it passes into the stomach. The ribbon occupies the entrance to the throat, moving backwards and forwards in the act of eating, and tearing the food to pieces.

Powerful protractor and retractor muscles control the working of the radula, or ribbon ; the food is seized by the chitinous jaws, and brought down on the radula, which with

a forward and backward movement rasps it off and conveys it into the œsophagus ; the radula is so thoroughly controlled that when protruded the points of the teeth are placed in a more or less vertical position.

The teeth are arranged in rows, and in many instances are very numerous ; in the common whelk they number from 220 to 250, in the periwinkle 2,500, in Helix aspersa about 30,000,

Fig. 167.—Teeth of Snail (*Testacella*).

and in Umbrella mediterranea they baffle calculation, possibly 750,000 may be somewhere near the truth.

They present varieties of pattern, but are usually serrated or pointed like the teeth of a saw, some of the cusps being larger than others ; in Buccinium undatum the broad central teeth are 6-cusped ; the teeth are attached to the ribbon of chitin, which occupies the floor of the mouth and throat, and are raised or depressed at will.

The teeth on the front of the radula are generally rounded and much worn, and finally lost, their places being taken by others from behind, suggesting the method of replacement in the calcified teeth of sharks and rays.

It is estimated by Sterki that during its life the Limax

campestris has eight entire changes of teeth. Some of the helices must have between sixteen and eighteen total changes.

Teeth of Fishes

General Characteristics of the Teeth of Fish.—Fishes are cold-blooded animals, living in water, breathing by gills (except Dipnoi, the mud fishes); they are oviparous, and the skin is usually scaly.

1. *Situation* of the teeth. Teeth are attached to the margin of the jaws in Elasmobranchii, cartilaginous fishes, e.g. skates, dog-fishes, and sharks; also in Ganoidei—e.g., the bony pike (*Lepidosteus*); but in Dipnoi, mud fishes, and Teleostei, the bony fishes, teeth are distributed all over the bones of the mouth and pharynx.

2. *Number.* Numerous, except sturgeon and pipe fish, which are edentulous.

3. *Form.* Usually alike in all parts of the mouth (homodont) with some exceptions, such as *Sargus*, *Cestracion Philippi* and *Anarrhichas Lupus*, where the teeth differ in form in different parts of the mouth (heterodont).

4. *Structure.* All forms of dentine; enamel forms tips of many teeth such as those of eel and hake. Tubular enamel is often present, such as in the teeth of *Sargus* and the Port Jackson shark (*Cestracion*). Cementum is rare, but is found in the socketed teeth of the Barracuda pike.

5. *Attachment.* All varieties; by fibrous membrane, in sharks, rays, and dog-fishes; hinge in pike, hake, and angler fish, anchylosed in the majority of fishes, socketed in Barracuda pike, and the rostral teeth of Pristis.

6. *Succession.* An endless series of teeth erupt throughout the animal's life (polyphyodont).

7. *Jaws.* Generally the closure is simple, but in hydrocyon the teeth interlock.

8. *Function.* Usually for prehension, not for comminution of food. Many fishes swallow their prey entire, but the molariform teeth of the Port Jackson shark and wolf-fish crush the shell cases of their victims.

Cyclostomata.—This sub-class represents a very ancient form of fish life, of which at the present time there are examples in the lamprey, myxine, and bdellostoma, all having circular sucking mouths.

They are not included among the true fishes owing to the absence of jaws.

Lamprey.—The rounded mouth of the lamprey is adapted for sucking and armed with a number of horny teeth, arranged in circular lines. In the centre are two larger ones, which gnaw into the flesh of the victim.

Myxine.—The myxine or hag is an eel-like parasitic creature, which attaches itself to the body of the cod and other fishes, subsequently boring its way into the stomach of its prey by means of a large horny median tooth above, and two rows of similar teeth below, on either side of the tongue, which act as lingual saws.

Bdellostoma.—Its habits are similar to those of myxine. According to Dr. Beard, the upper median tooth is composed of horn, superimposed upon a calcified structure, resembling coarse dentine, but this view is considerably disputed.

The Orders of Fishes

I. **Elasmobranchii** are cartilaginous fish; the skin is covered with calcified scales (shagreen), which are homologous with teeth. They are represented by sharks, dog-fishes and skates. This order, together with the Ganoids, of which the sturgeon and bony pike are examples, appeared very early in geological time, and was the dominant form of fish life throughout the Secondary (Mesozoic) period, and has persisted to the present.

Sharks.—(*a*) (1) *Situation of the Teeth.*—They are attached to the margin of the jaws, a row of upright teeth occupying the summit constantly recruited by successional teeth from behind.

(2) *Number.*—Very numerous.

(3) *Form.*—The teeth are triangular, flattened blades, very sharp pointed, sometimes with serrated margins, bifurcated at the base, and roughened for attachment to the fibrous membrane.

(4) *Structure.*—The greater portion of the tooth consists of osteo-dentine, with elongated lacunæ, which, on the surface, merges into tubular dentine. A film of structureless vitro-dentine covers and protects the tooth; this tissue resembles enamel, and was formerly mistaken for it. The enamel of orodus and carcharodon, two extinct sharks, is penetrated by a system

of tubes from the surface of the dentine ; and in another instance by tubes penetrating from the exterior of the tooth, as is also the case in the modern Port Jackson shark. In the early extinct cestraciont sharks of the Carboniferous period, plici-dentine was the principal structure. This is well seen in the section of the tooth of Rhizodus, with the numerous channels of pulp (Fig. 128).

(5) *Attachment* by a fibrous membrane to the cartilaginous jaws. In sharks the jaws are cartilaginous, covered with a partly ossified crust, to the margins of

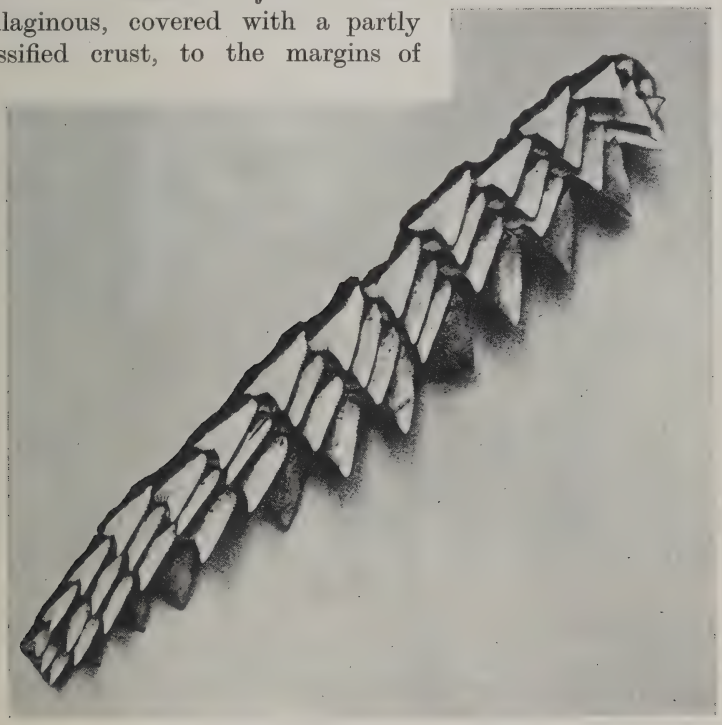


Fig. 168.—Reserve teeth of Shark.

which numerous teeth are attached by a fibrous membrane. Behind the upright row of teeth in position there are numerous other rows, one behind the other, covered and concealed by a flap of mucous membrane. When a tooth is lost from the summit of the jaw, a reserve one from behind rises and occupies the position of the missing tooth. The whole series of reserve teeth gradually rise, and are

carried upward by a rotating movement of the mucous membrane, so that the teeth from the base are borne upwards, and in time they occupy the crests of the jaws.

The teeth constantly fall off, and become embedded in the mud of the floor of the ocean, where they are subsequently fossilized.

(6) *Succession.*—Polyphyodont.

(7) The jaws and mouth form a transverse aperture ; at the entrance is a marginal row of teeth on the partly ossified covering of the cartilaginous jaws.

(8) *Function.*—This formidable dentition is used by the

Fig. 169.—Dentition of Shark (*Cestracion philippi*).

predacious sharks for securing and tearing their prey. In the Australian seas is a curious little shark, *Cestracion philippi*, measuring about five feet in length, the representative of an extinct group which was once very numerous.

The fossil teeth of Cestracionts occur in the Carboniferous rocks, some of them, such as orodus, were of great size, and resemble those of the Port Jackson shark of the present day. Their food consisted of crustaceans and hard-shelled animals, for which the dentition was well adapted.

Seven or eight rows of sharply pointed teeth, designed for seizing prey, occupy the front of the jaws, and large molariform teeth the back, for crushing purposes, the largest in the centre of the series.

Dog-fish.—The skin of the dog-fish, like that of the shark, is covered with calcified papillæ, which carry sharp-pointed spines, known as shagreen, and have the same microscopical structure as teeth.

In the development of the young dog-fish the outer skin or epidermis is continuous with the inner skin or epithelium covering the interior of the mouth, and there is no break in continuity over the forming jaw. The external spines and internal teeth originate from the same tissue, and are identical in shape and structure, leading to the conclusion, confirmed

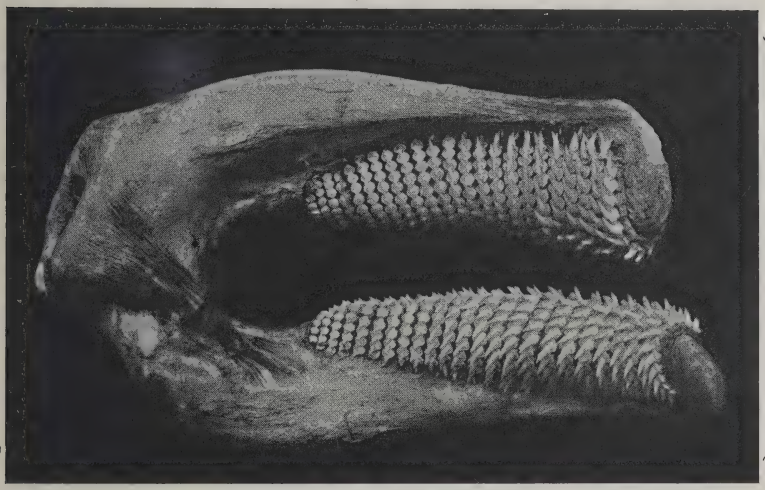


Fig. 170.—Dentition of Thornback Ray (*Raia clavata*).

by embryology, that teeth are but modified dermal spines. The succession is endless, as in the shark, new germs being constantly given off from the base of the tooth-band.

The Rays or Skates are large flat fish, very common near the shore line, voracious in their habits, and feeding on molluscs and crustaceans. Embedded in the skin of the thorn-back ray are numerous large, recurved and sharp-pointed spines, known as placoid scales. Each has a structure of dentine covered with enamel, the base being bony, so that in form and structure they are identical with teeth. The jaws of the thorn-back ray are covered with a mosaic pavement of small closely fitting rounded teeth in the female, while in the male they

are pointed, a curious illustration of a sexual difference in the teeth of fishes.

Myliobates.—In the eagle ray (*Myliobatis aquila*) the dentition consists of numerous flat hexagonal plates, the central row being long and powerful, fitting into smaller teeth of the same character arranged in lateral rows. The whole forms a most efficient crushing apparatus.

Ætobatis resembles myliobatis, but the plates are broad and flat, forming a single series, each plate being bent instead of straight as in the former.

Fig. 171.—Dentition of Myliobates.

Structure.—The tooth plates of myliobatis are built up by the coalescence of numerous denticles, parallel, and free at the base, where they resemble the teeth of a comb, united on the surface into a pavement, homogeneous and flattened, which in section shows a beautiful plici-dentine structure.

The plates are attached to a dense fibrous gum, as in the sharks, which may be stripped entire from the jaws.

Ptychodus.—The rays attained their greatest size in the ptychodus of the Chalk period.

The teeth are beautiful examples of adaptation for crushing

purposes. The surface of the crown is covered with four or five lofty and sharp ridges separated by deep valleys; the circumference is crowded with small rounded cusps, which give a grip and prevent the slipping of a crustacean, a tooth admirably fitted for its work. Structure, plici-dentine.

The Saw-fish (*Pristis*), a family of rays, has the usual oral dentition of numerous minute, rounded teeth attached to a fibrous membrane.

It is also provided with a powerful weapon of offence, in the elongated spatula-shaped snout, which is armed with strong flattened, pointed teeth, fixed in deep sockets which grow from persistent pulps, a feature of special interest.

The saw is often capable of inflicting severe wounds, and attains a great size, sometimes exceeding six feet in length.

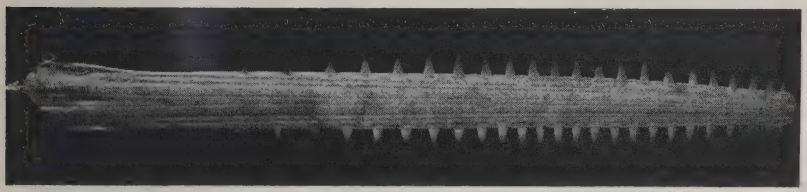


Fig. 172.—Rostral teeth of Saw-fish (*Pristis*).

The saw-fish is said to use this weapon for attacking its prey, tearing open the abdomen and devouring the entrails. The structure of the rostral teeth is plici-dentine, the matrix being penetrated by a series of parallel canals of pulp with their ramifying dentinal systems; a small quantity of cementum is found on the roots, which is rare in fishes.

II. **Ganoidei.**—The Ganoids, a class of fishes largely represented in Mesozoic times, are now illustrated by the bony pike (*Lepidosteus*) of North America, and the sturgeon (*Acipenser*).

Lepidosteus.—The body is completely enveloped in lozenge-shaped scales. The narrow beak-like jaws are furnished with bands of rasp-like teeth, a few larger than the others; they are partly socketed, with a thin covering of cementum on the implanted roots. The structure of the tooth is plici-dentine.

Sturgeon.—The body is protected by five rows of bony

buckler plates, the mouth is edentulous, though it is said to possess teeth in the larval state.

III. **Dipnoi** (*lung breathers*).—Ceratodus, the Australian mud-fish, inhabits the rivers of Queensland, and is provided with gills and a lung, and can live in water or on the land. It is stated that occasionally the fish leaves the rivers to frequent the mud flats for a time. Ceratodus is one of the few remaining specimens of the primitive group Dipnoi, the lung-

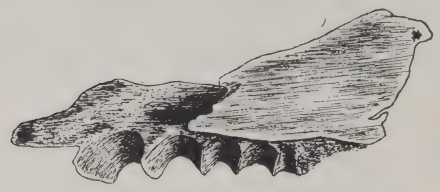


FIG. 173.—Dental plate of Ceratodus.

FIG. 174.—Dentition of Sea Perch (*Serranus Cabrilla*).

breathing fishes which appeared first in the English Devonian rocks.

The dentition consists of two incisor-like teeth in the front of the upper jaw, while behind, lining the margin, are two large

serrated plates covered with enamel, which meet in the median line of the palate, and are opposed by similar plates in the lower jaw; the deep notches interdigitate in the act of eating the aquatic plants which form its food. The plates are anchylosed to the bone (Fig. 173).

Lepidosiren, the African mud-fish, possesses a similar dentition.

The Dipnoi suggest a link between fishes and batrachians.

Fig. 175.—Setiform teeth of Catfish (*Arius*).

IV. **Teleostei.**—The Teleostei, which constitute the dominant fish life of the present time, date back to the Chalk period. They have ossified skeletons, with completely formed vertebræ, and are usually covered with soft scales. The teeth are distributed over the bones of the mouth and pharynx, the gill bones and base of the tongue being often so armed, as in *Serranus* (Fig. 174).

The primitive tooth form is conical, and they vary from the simple, bristle-like (setiform) teeth, which cover the palate of the catfish (*Arius*), Fig. 175, having together the appearance of a bristle brush, to the powerful conical teeth in the front of the jaws of the gilt-head (*Chrysophrys laticeps*) and wolf-fish (*Anarrhichas lupus*), Fig. 180.

The fishes which swallow their prey whole are typically seen in the pike, angler-fish and cod, which are furnished with sharp pointed conical teeth.

The *Pike* (*Esox lucius*), Fig. 176, possesses three bands of small hinged teeth in the upper jaw, attached to the vomer and palatine bones. On the latter the hinges bend inwards and backwards, while on the vomer they bend outwards and backwards. This arrangement enables its prey to be grasped and swallowed, passing readily over the teeth, which bend to assist its progress, and immediately afterwards the teeth resume their upright position, effectually preventing the escape of the

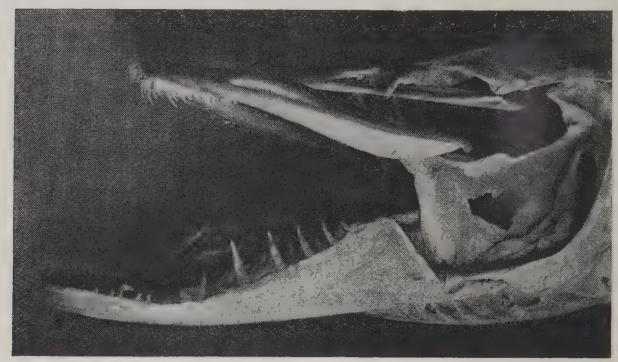


Fig. 176.—Jaws of Pike (*Esox lucius*).

captured fish. The hinge is of an interesting character, occasioned by elastic rods, or trabeculæ, attached to the bone and underside of the tooth, and always remain uncalcified. They stretch when the tooth is in use, and afterwards return it to its original position (Fig. 192, 2).

A few small teeth are anchylosed to the front of the upper jaw.

In the back of the lower jaw on either side three or four large compressed sharply pointed teeth are anchylosed by a special bone of attachment, upon the points of which the prey is impaled; the struggles of the victim only serve to drive the powerful teeth deeper into its body.

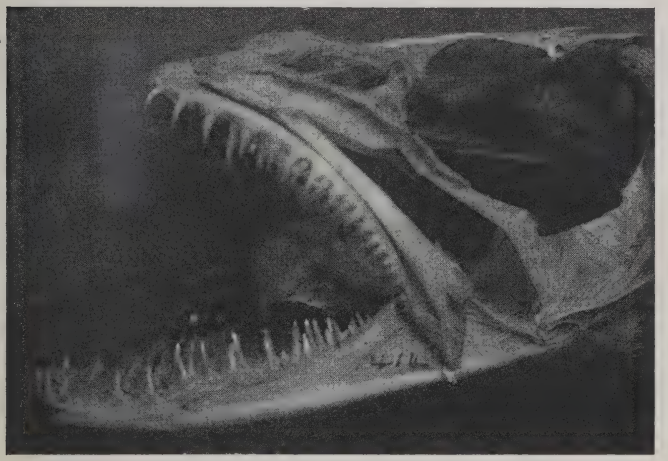
The gill bones are also covered with numerous sharply pointed teeth.

The large lower teeth are formed of osteo-dentine, which towards the surface becomes converted into a fine tubed dentine, covered by a film of structureless vitro-dentine.

The Angler-fish (*Lophius piscatorius*) inhabits the British coasts, where it sometimes attains a length of five feet, and is a singular-looking fish, with an enormous head in proportion to its body. The name angler is given from its habit of lying in wait for its prey, with its body concealed in the mud. It attracts small fishes by dangling in front of its capacious mouth a lure, with a worm-like appearance, attached to the end of a long filament.

Its body has become profoundly modified and the fins are rudimentary.

The dentition is remarkable, the great jaws being armed with



[Fig. 177.—Jaws of Hake (*Merlucius*).

powerful conical recurved teeth, the outer row anchylosed and the inner hinged. These bend backwards when its prey is captured, afterwards returning to their original position, and so rendering escape impossible; the largest teeth are in the centre of the sides of the mouth. The elastic fibres which tie the tooth down to the bone are attached fanwise.

Structure of teeth, unvascular ortho-dentine.

The Hake (*Merlucius vulgaris*), one of the cod family, has two rows of sharp pointed teeth on the margin of each jaw, the outer anchylosed and the inner hinged. The teeth are red when the fish is first caught, from the numerous blood capillaries which permeate the matrix, and are seen in section as loops just underneath the surface, constituting a typical vaso-

dentine, in which the blood circulates ; the apex of the tooth is capped with an enamel spear point (Fig. 130).

The *Water-dog* (*Hydrocyon*), a predatory fish inhabiting the Congo and other tropical African and South American rivers, is one of the most ferocious of existing fishes. The jaws are

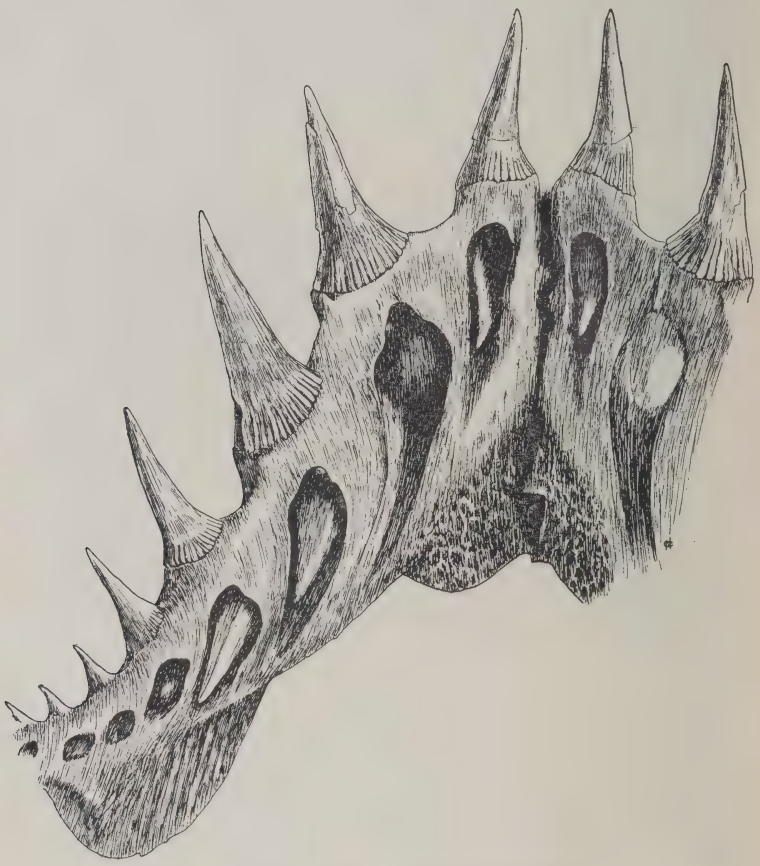


Fig. 178.—Reserve teeth of Water-dog (*Hydrocyon*).

very strong, each armed with a single row of triangular knife-edged teeth of great size anchylosed to the bone and fluted at the base. There are wide intervals between the teeth, in which the opposing teeth interdigitate in closure, and spaces are hollowed in the bone opposite to accommodate them. There are no teeth on the palate.

The displacement is especially interesting, for in the life of this fierce and powerful fish the tooth germs would be especially liable to injury. They are accommodated in large bony crypts at the base of their predecessors, and lie in a horizontal position effectually protected, and subsequently rise upwards into place when the older teeth are lost. This arrangement is reminiscent of the replacement of the poison fangs in a viperine

Fig. 179.—Canine-like teeth of Chilinus.

snake. When erupting, the orifices of the crypts are widely opened by absorption to allow for the emergence of the teeth. In some fishes a pair of canine-like teeth are present in the upper jaw. This is noticed in *Chilinus*, a wrasse of the China Sea, where a pair of caniniform teeth in each jaw are visible.

The jaws of the *Barracuda pike* (*Sphyræna*) are furnished with a single row of powerful sharp pointed lancet-shaped teeth, and in the front of each jaw are two pairs, one behind the

other, recurved, for seizing and holding their prey. The Chirocentros offers a similar example; the front of the lower jaw carries numerous long scimitar-shaped teeth for capturing fish. The marginal teeth increase in size towards the back of the mouth, being socketed, and slightly attached to the wall of the sockets by anchylosis. The roots are covered with a film of cementum.

The jaws of the *Gar-pike* (*Belone*) are developed into a long

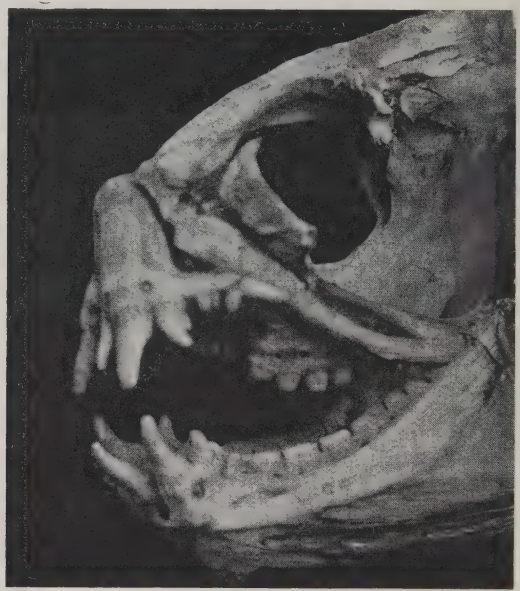


Fig. 180.—Teeth of Wolf-fish (*Anarrhichas lupus*).

and narrow beak, beset with sharp pointed conical teeth; the intervals between them are occupied with minute setiform teeth.

The *Wolf-fish* (*Anarrhichas lupus*) is a large fish, coastal in its habits, inhabiting the shores of Britain. Its diet consists of shell-fish and crustaceans, for which the teeth are specialized.

The jaws are stout and powerful, carrying in the front of the mouth several large conical fluted teeth anchylosed to the bone, for seizing its prey, and on the vomer and palatine bones double rows of large molariform teeth for crushing purposes, which are opposed to similar teeth in the lower jaw.

Cavities are visible at the base of the permanent teeth for

the accommodation of tooth germs for their successors, which by absorption excavate their way into the interior of the older teeth, and ultimately displace them.

Structure, plici-dentine.

The *Gilt-head* (*Chrysophrys laticeps*) is a somewhat similar example, where the teeth are adapted for the same habits.

Structure, ortho-dentine, the inner part of the enamel being permeated with a meshwork of crossing tubes.

The *Sheep's-head fish* (*Sargus ovis*) has, in the front of the mouth, curious teeth shaped like human incisors, eight above and six below, for tearing off shellfish from the rocks; these are subsequently crushed by the rounded molars at the back, arranged in several rows varying in size and anchylosed. The front teeth are fixed in sockets and displaced vertically from within the jaw bone.

Fig. 181.—Gymnodont teeth of Tetrodon.

Structure, ortho-dentine, enamel penetrated by tubes from the exterior, developing internally into an intercrossing meshwork of fibres (Fig. 95).

The *Gymnodonts*, or naked-toothed fishes, are represented by the globe fishes, *Diodon* and *Tetrodon*. In this class the front of the mouth has a beak-like shape, from the fusing of the bone and dental tissues, giving the appearance of two teeth in the diodon, and four in the tetrodon. A pavement of the same material for crushing purposes exists on the floor of the mouth, opposed by a similar arrangement in the upper jaw, built up by hori-

zontal plates of dentine, formed beneath the surface, which replace the older plates when worn away.

Structure, osteo-dentine, from the fusing of the bone with the old and new plates of dentine.

For defensive purposes the body of the globe-fish is covered with powerful spines, somewhat resembling the teeth of the shark, which can be elevated when the creature is alarmed by distending the body into a globular shape. In structure they resemble teeth.

Parrot-fish (*Scarus*).—The same arrangement holds good with the parrot-fishes, where beak and dental pavement are formed by the fusion of tooth and bone, resulting in a roughened surface of various degrees of hardness.

Structure, osteo-dentine.

In the *Chub* and the *Barbel* the mouth is edentulous, but the strong pharyngeal bones are furnished with large conical pointed teeth attached by anchylosis. The successional tooth germs are fitted into depressions hollowed out to accommodate them, at the base of the teeth on the inner surface. The pharyngeal teeth interdigitate in the act of mastication, comminuting the food as it passes into the stomach.

CHAPTER XII

THE TEETH OF AMPHIBIA AND REPTILES

Amphibia

The amphibia connect fishes with reptiles, breathing with gills at one period of existence and lungs at a later stage; they appeared first in the Carboniferous period, where they were represented by many large and varied forms. Now the class numbers few representatives; it includes our toads and frogs, newts and salamanders.

The *Toad* is usually edentulous, but a few tropical specimens retain one or two teeth in the lower jaw.

In the *Frog* the margin of the upper jaw is lined with a row of small pointed teeth, formed of hard dentine, covered by a thin film of structureless enamel; the edentulous lower jaw closes immediately behind them. The successional teeth are formed from germs situated below the existing teeth, which they displace by gradual absorption of the base. The teeth of newts and salamanders are protected by bifurcated tips of enamel.

Labyrinthodon was a gigantic amphibian, rivalling the alligator in size, which existed in the Palæozoic and Mesozoic periods. Its fossil remains show that the margins of the jaws were lined with large fluted teeth, a single row in the upper jaw, and double in the lower, with a few teeth on the palatal bones; they were attached by anchylosis to shallow sockets. In the upper jaw some were tusk-like in appearance. The complex structure of the tooth has suggested a name for the creature from the labyrinth-like character of the plici-dentine, as seen in a transverse section of the tooth. Each branch of the pulp starts from the central chamber and pursues a serpentine course towards the periphery of

the dentine, giving off its series of inosculating dentinal tubes, and producing the labyrinth-like appearance of the structure.

Reptilia

General Character of the Teeth of Reptiles

1. *Situation.*—The teeth are reduced in number in reptiles and are generally situated on the margins of the jaws, and sometimes on the vomer and palate bones, forming a double row above, with a single row in the lower jaw, biting between or interlocking in closure.

2. *Number.*—The number is very variable; numerous in crocodiles, lizards and pythons; reduced in number in viperine snakes.

3. *Form* is usually homodont, recurved cones compressed in lizards, margins crenated as in the iguana, or sharp-pointed as in python.

4. *Structure* is usually ortho-dentine, protected by enamel, and in one instance, the crocodile, the implanted portion of the tooth has cementum, a rare occurrence. Plici-dentine forms the base of the tooth in the monitor lizard (*Varanus*).

5. *Attachment.*—In almost all cases the attachment is by anchylosis, a special rough coarse bone uniting the tooth to the jaw and called the bone of attachment, which is removed by absorption when the tooth is lost. This is especially evident in snakes, where the teeth are liable to be broken by the force used in capturing and killing their prey, and the bone has to be prepared for the reception of the succeeding teeth. The crocodile is an exception—its large conical teeth occupy deep sockets, to which they are attached by a fibrous periodontal membrane.

6. *Succession.*—Polyphyodont, but in the chameleon and sphenodon there is no replacement of teeth.

7. *Jaws.*—In the upper jaw the teeth are confined to the intermaxillary, maxillary, palatal and vomerine bones, often forming a double row between which the lower teeth close, as seen in the python. The lower jaw consists of several bones united together; this characteristic serves to distinguish fossil jaws of reptiles from mammals.

8. *Function.*—The teeth of reptiles are generally used for the prehension and not the comminution of food. In venomous snakes a pair of teeth in the upper jaw are enlarged, grooved or canaliculated for use as poison fangs to convey venom into the wound made by the long and sharp pointed teeth.

Fig. 182.—Jaws of Crocodile.

Chelonia. — The Chelonia, comprising the turtles and tortoises, are all edentulous. In place of teeth the jaws are provided with a horny covering, sharp edged or serrated in carnivorous varieties, and rounded in herbivorous species.

The **Crocodilia** are represented by crocodiles, caimans and alligators, and are descendants of a very old group of reptiles. The powerful jaws of the crocodile are armed with numerous large pointed conical teeth fixed in sockets, an unusual characteristic in reptiles. In closure the teeth interlock, the first lower pair perforate and are

received into holes in the intermaxillary bone, and the fourth lower tooth into a notch in the upper jaw (Fig. 182).

The number of teeth is constant for each species and certain ones are enlarged. The jaws of the gharial of the Ganges are attenuated and elongated, the teeth recurved and sharp-pointed, well adapted for seizing fish; they number 118, and do not vary in size.

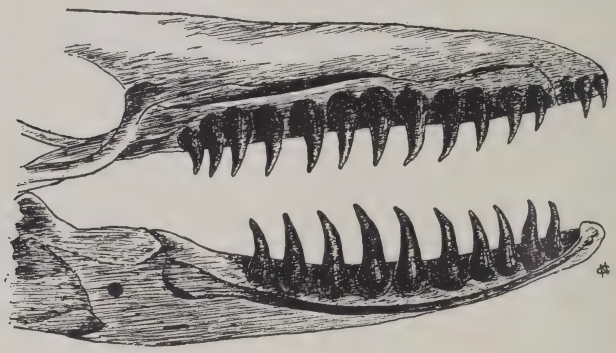


Fig. 183.—Dentition of Monitor Lizard (*Varanus*).

Alligators and caimans possess a dentition of seventy-six; the fourth lower tooth in closure fits into a pit and not into a notch as in the crocodile.

Structure.—The teeth of the crocodile are formed of ortho-dentine, with a thin covering of enamel, the embedded portion having a thick layer of cementum.

Succession.—The successional tooth germ lies at the base of the tooth in position; in eruption the side of the tooth is rapidly excavated by absorption, and the wall ultimately penetrated, when the germ enters the pulp cavity and speedily displaces, vertically, its predecessor. Frequently it carries two or three of the older teeth as hollow, extinguisher-shaped cylinders, which have been successively displaced; the process is repeated throughout the life of the crocodile. This method was anticipated by the ichthyosaurus, a marine lizard of the Mesozoic period, whose fossil teeth show evidence of this form of succession.

The **Lacertilia** or lizards of the present are puny compared with the monstrous saurians of old, the largest living representative being the monitor lizard (*Varanus*) of the

tropics, which occasionally reaches a length of five or six feet; its food consists of eggs, fruit and insects.

Its teeth line the margins of the jaws, in a single row; there are about thirty in each jaw, flattened, scimitar-shaped, sharp-pointed, fluted at the base, the largest teeth are on the sides, and a few small ones are found on the palate (Fig. 183).

The structure is ortho-dentine at the summit and plici-dentine at the base. They are attached to the inner alveolar plate. Crypts for the successional teeth are seen at the base of each tooth; the replacement is polyphyodont.

Fig. 184.—Sphenodon (*Sphenodon punctatus*).

The crowns vary in shape in different lizards. Some are simple and rounded, others have crenate or serrate margins, and are attached to the jaw, either anchylosed to the summit of a pedestal of bone, acrodont attachment, or to an external parapet of bone, pleurodont attachment.

The *Mexican Lizard* (*Heloderma*) has the evil reputation of being the only venomous member of this class; its bite is fatal to small mammals, and very poisonous even to man. Some of its teeth are grooved before and behind for the transmission of the poison and they resemble the poison fang of the snake.

The *Chameleon* has only one set of teeth which are not replaced, and hence is monophyodont.

Rhyncocephalia.—There is only one modern representative of this section, the sphenodon (*Tuatera punctata*). It is the only survivor of a group of primitive reptiles, which existed in the age of the Trias. It inhabits New Zealand and the adjoining small islands and measures one to two feet in length.

The jaws are narrowed in front resembling a beak, and in the premaxillary bones a pair of sharp-edged teeth are anchylosed to the margin, resembling the incisors of a rodent. Each tooth, however, is formed of three small teeth fused together, opposed by similar teeth in the lower jaw (Fig. 184).

In this reptile there is no replacement of teeth, therefore the dentition is monophyodont.

After considerable wear of the front teeth the surface of the bone becomes exposed and used for mastication, a very unusual occurrence.

The numerous small rounded side teeth attached in an acrodont fashion are lost early in life.

Ophidia.—Snakes.—This group may be divided into four families: 1. Typhlopidæ. 2. Boidæ. 3. Colubridæ. 4. Viperidæ.

Typhlopidæ, represented by small worm-like burrowing snakes, which have vestigial eyes, and no teeth in the lower jaw; they are of insectivorous habits.

Boidæ.—In this family are included the boas and pythons, which kill their prey by constriction. They sometimes retain vestiges of the pelvis and hind limbs in rudimentary claw-like structures, proclaiming their descent from four-footed ancestors. Most of them are of large size; a Malay python in the Natural History Museum at South Kensington measures nearly twenty-five feet. No member of this family is venomous.

Dentition of Boidæ.

1. *Situation and Number of Teeth.*—In the upper jaw there

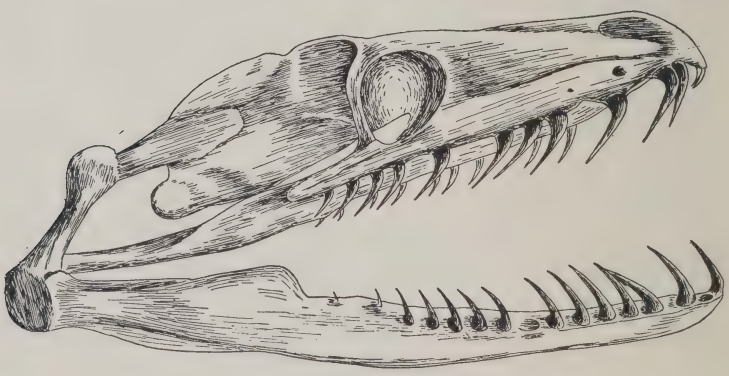


Fig. 185.—Jaws of Python.

is a marginal row of numerous teeth and an inner row on the palatine and pterygoid bones; the premaxilla is edentulous in the boa but not in the python. The margin of the lower jaw is furnished with a series of similar teeth.

2. *Form.*—They are conical, recurved, haplodont, with an abrupt bend, very sharply pointed and differ but little in size.

3. *Structure.*—The teeth are formed of hard dentine and enamel, no cementum is present.

4. *Attachment.*—They are anchylosed to the bone by a coarse bone of attachment.

5. *Succession.*—The successional tooth germs lie in a horizontal position near to the bone in a capsule of connective tissue, and afterwards assume an upright position to replace their predecessors. The method by which this is accomplished is not known.

6. *Shape and Movement of Jaw.*—The mouth is expansible, maxillæ, palatines, and pterygoids are movable, and the two halves of the mandible are attached by elastic ligaments. Added to this the quadrate bone at the back of the mouth provides an additional hinge, which permits the creature to distend the jaws to a great extent to seize and swallow its prey. The snake grasps its victim head first, and when seized by the needle-pointed hooked teeth the jaws alternately move forwards and its prey is gradually drawn inside its captor's body. The snake literally gets outside its quarry. The process is slow and absolutely mechanical, as each jaw in turn relaxes its grip, only to travel forwards for an additional hold, so that anything once seized is bound to be swallowed. The teeth of the python are used by fishermen on the Congo for fish-hooks.

Colubridæ are divided into—

(*a*) *Aglypha.*—The teeth are numerous, solid and ungrooved, and of similar size ; these snakes are non-venomous. The common British grass snake is an example, as is also *Dasypeltis scabra*, an African egg-eating snake, in which the mouth is edentulous, but spinal processes from the cervical vertebræ penetrate the shell when the egg is swallowed.

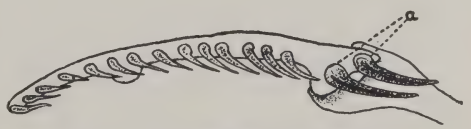


Fig. 186.—Opisthoglyphous snake.
a, Grooved posterior poison-fangs.

(*b*) *Opisthoglypha.*—One or two of the hinder upper teeth are grooved.

In this sub-family is witnessed the first stages in the development of the poison fang.

In the upper maxilla the two hinder teeth are much enlarged, with a widely open groove running down the anterior surface for the transmission of the poison ; instances of this character are seen in the Indian tree and whip snakes. The change from the solid, unspecialized, harmless teeth, with the innocuous parotid secretion of the Aglypha is evident in Erythrolamprus, a snake which, though belonging to the class Opisthoglypha, possesses an aglyphous dentition. Though the two hinder teeth on the maxilla are enlarged there is an entire absence of a groove, but in spite of this the bite of the snake is venomous.

The widely open furrow running from base to point of the two enlarged teeth in some cases becomes deepened into a channel, the two edges of which gradually converge.

(c) *Proteroglypha.*—The maxillæ are shortened, the teeth on the maxillary bones are greatly reduced in number, the anterior tooth being enlarged and grooved in front for conveying the venom to the wound. The cobras, kraits and Indian sea snakes (Hydrophis) are examples. All the members of this sub-family are dangerous to man. The bite of Hydrophis is especially deadly, far more dangerous than the cobra ; it is the terror of the Malay fishermen. In Hydrophis the poison fang is deeply grooved, but in the cobra the lips have met, forming a canal. The maxilla of the cobra moves slightly so that the teeth are not fully erect when the mouth closes, but fit into a groove in the lower lip. The poison fang is replaced from a single series of successional teeth, enclosed in a fold of mucous membrane behind the poison tooth, one being fully formed, ready to move forward, and occupy the place of the lost tooth, and behind are others in different stages of development.

FIG. 187.—Proteroglyphous snake.
a, Poison-fangs.

VIPERIDÆ includes puff adders, vipers and rattlesnakes. In these snakes the maxillary bones are greatly reduced in size, being just large enough to accommodate a single poison fang in each bone with space by the side for a successional tooth in case of injury to the one in position. The dentition is diminished to one large venom tooth on either side of the

mouth, canaliculated for transmitting the poison. The opening to the canal is seen on the anterior surface at the base of the tooth, opposite the duct of the parotid gland. The end of the fang is thinned to an exceedingly sharp point of dentine,

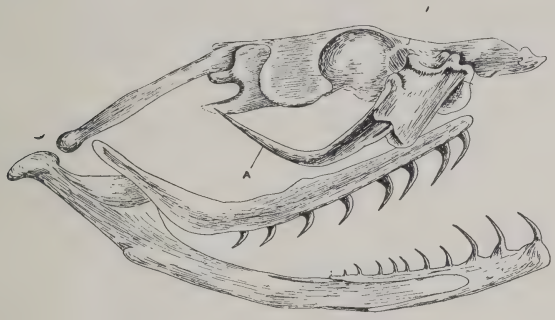


FIG. 188.—Puff adder (*Bitis arietans*).
A, Poison-fang.

covered by enamel, the exit from the canal through which the poison is ejected lies immediately above it.

A microscopic section of the tooth shows that the canal is formed by the union of the edges of the deep groove noticed in the cobra; the fusion is so complete that externally there

FIG. 189.—Reserve fangs of Puff adder.

is no sign of the union. The same fact may be observed in the developing fangs, which in their early stages show the canals open and unenclosed.

The extreme length of the fangs renders them liable to be broken off when the rattlesnake or puff adder strikes and embeds the teeth in the body of its victim, whose struggles frequently lead to the loss of one or both fangs. Successive fangs are provided in different stages of development enclosed

in a fold of mucous membrane, which lie in two parallel series behind the tooth in position in a horizontal fashion, numbering ten in the rattlesnake. One or two are always complete, formed ready to move up to occupy the bare space on the maxillary bone to the right or left of the lost tooth. In the Proteroglypha, e.g. in the cobra, the series is more limited in number, the successional fangs being single, lying one behind the other.

In the viperine snakes the reduced maxillary bone acts as a hinge, and when not in use the large poison fang is concealed

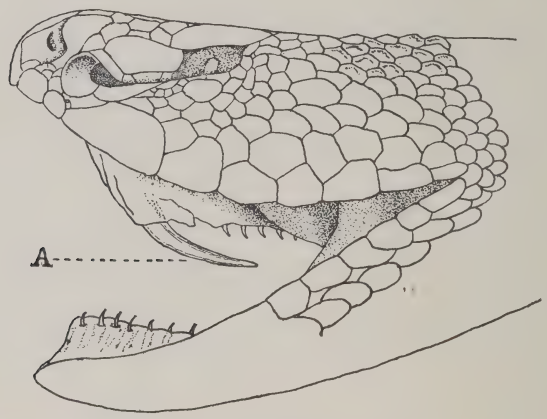


Fig. 190.—Viperine snake.
A, Poison-fang.

from view, lying along the roof of the mouth, to be out of the snake's way in eating. When the mouth opens the hinged maxilla is pushed forwards, and the tooth becomes vertical, in readiness to be plunged into the body of its victim, forcing a jet of poison through the large canal. The hypodermic syringe is fashioned on the pattern of the viper's tooth.

The poison being the secretion of the parotid gland varies in intensity in different snakes; the glands are smaller in the less specialized varieties.

The degree of the virulence of the venom also varies in different snakes. That of the rattlesnake is of so deadly a character that death has resulted in a rabbit within a minute after being struck, and the poison is as fatal to other snakes as to mammals, but that of the dreaded sea snake Hydrophis

is of the deadliest nature, from five to twenty times stronger than in other venomous snakes.

The evolution of the poison fang with its complex mechanism is an interesting study, as we trace step by step the gradual reduction in number of the maxillary teeth, shortening of the jaws, the guttering, grooving, and canaliculating of one special tooth for its deadly purpose.

Contrast in the Dentition of Proteroglypha

1. Situation and number.

(*a*) *Hydrophis :* five or more teeth are on the maxilla, the

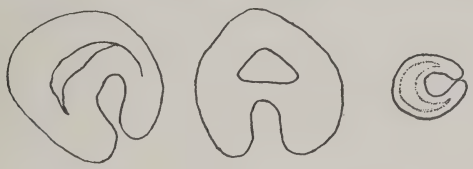


Fig. 191.—Evolution of poison canal.
A, groove ; B, groove closing in ; C, canal.

anterior being the largest and grooved for a poison fang : also a row of teeth on the lower jaw.

(*b*) *Cobra :* a poison fang is on the maxilla, with two or three smaller teeth behind it : also a row on the palatine and pterygoid bones, as in python, and a single row on the lower jaw : all these are simple recurved cones.

(*c*) *Viper :* only one poison fang is on the maxilla : behind is a single row on the pterygoid and palate bones, and a single row on the lower jaw, all simple recurved cones.

2. Form of the poison fang.

(*a*) *Hydrophis :* deeply grooved.

(*b*) *Cobra* : lips of groove have met to form canal, but the line of junction is visible from the outside as rounded lips ; the fang is about $\frac{1}{4}$-inch long.

(*c*) *Viper :* canal completely formed and the line of junction of groove not visible : fang an inch or more long and the lower entrance to the canal not at the tip, but oblique as in the hypodermic needle.

3. Structure of poison fang.

In all three is ortho-dentine, continued down to a very fine point, with only a thin covering of enamel : an enamel tip, such as we find in fish, would break in a snake. No enamel is

inside the canal, and the pulp chamber is horse-shoe shaped.

4. Attachment.

In all three anchylosed by bone of attachment.

5. Succession.

(*a*) *Cobra:* endless succession from a single series of tooth germs, arranged vertically, but the front of the maxilla is wide enough for two teeth; and successional teeth from the single series erupt to right and left alternately. This ensures rapid replacement: sometimes if the tooth is not lost quickly two fangs are found erupted side by side.

(*b*) *Viper:* maxilla wide enough for two fangs, but in this case there is a double series of tooth germs arranged vertically and separated from each other by a flap of mucous membrane: functional tooth recruited from each series alternately to ensure quick replacement: sometimes two functional teeth found side by side. This succession of a single tooth from two series of tooth germs is unique.

6. Shape and movement of jaws.

(*a*) *Hydrophis:* maxilla moderately short and fixed.

(*b*) *Cobra:* maxilla shortened and slightly movable so that when the mouth is closed the fang is not fully erect and fits into a groove in the lower lip.

(*c*) *Viper:* maxilla very short and hinged to skull: the closure of the mouth automatically pulls the maxilla back and rotates it, so that the fang lies along the roof of the mouth; opening of mouth reverses the process and erects the fang.

7. Function of poison fang.

(*a*) *Hydrophis:* poison most deadly of all: guided into the groove by lip stretched tightly over it.

(*b*) *Cobra:* poison guided into canal by flap of mucous membrane, but some escapes outside.

(*c*) *Viper:* mechanism as in cobra, but more perfect, and all poison travels down the canal.

Extinct Orders of Reptiles.—The Mesozoic or middle period of geological time was essentially the age of reptiles, when great varieties, some of immense size, peopled the earth and formed the dominant life.

They anticipated the subsequent division, which took place in the mammals, of separation into flesh, leaf and insect eaters, great representatives of all these classes being found in the

Dinosaurs (*Deinos* Gr., *Sauros* Gr., terrible lizards) of that period.

Herbivorous Dinosaurs were represented by the *Diplodocus*, a monstrous creature measuring 80 to 90 feet in length, 14 to 16 feet in height, whose restored fossil form is seen in a cast in the Natural History Museum at South Kensington. It lived probably on the abundant aquatic vegetation then present.

The teeth are small and feeble for an animal of such great size, but the method of succession is very interesting, reminding one of the replacement of the poison fangs of snakes; at the base of each permanent tooth is a series of others, one beneath the other, in different stages of development.

The *Iguanodon*, a gigantic herbivorous lizard, stood probably 30 feet in height, the body supported on its massive hind legs, like the kangaroo.

An illustration of it is seen at South Kensington, and at the Brussels Natural History Museum a whole gallery is occupied by examples of this strange creature, excavated from the neighbouring mine of Bernissart.

The jaws in front were covered with horn, like the turtle, at the back numerous large teeth occupied the molar region, with rounded crowns and crenulated margins like those found in the little iguana of Mexico, hence its name of iguanodon, the structure being vaso- and ortho-dentine.

Carnivorous land forms are illustrated by the *Megalosaurus*, whose formidable sickle-shaped teeth indicated the carnivorous habits of the reptile. *Ichthyosaurus* and *Plesiosaurus* were marine saurians of the Jurassic period, measuring in some instances 40 feet in length, their jaws armed with numbers of large conical teeth, sharp pointed, with fluted sides. Those of Ichthyosaurus were flat bottomed, standing in an open gutter of bone, not fixed in separate sockets; only about a third of the tooth projected above the jaws, the greater portion being embedded in the alveoli. They interdigitated in closure and were replaced like those of the modern crocodile, the successional tooth germs burrowing their way into the sides of the older teeth, which they ultimately displaced. The structure of the tooth of Ichthyosaurus is plici-dentine, from the folding of the blades of pulp caused by the wrinkling or fluting of the surface, resembling the spokes in a wheel.

Anomodont Reptiles.—During recent years remains of strange reptilian forms have been brought to light in the Trias of South Africa, which have been grouped into two divisions, Therochelonia and Therosuchia.

In the first, THEROCHELONIA, the jaws were entirely covered with horn, somewhat resembling the modern turtle, and in others as the *Dicynodon*, two tusk-like teeth resembling canines were also present in the horny jaws.

The second group, THEROSUCHIA, has far the greatest interest, for in it are found reptiles, styled *Theriodontia*, possessing a heterodont dentition, thus anticipating by myriads of years the specialized teeth of the mammals that followed them.

Many authorities consider that the Theriodontia may probably be the ancestral line from which mammals originated.

Two examples may be quoted.

In *Ælurosaurus* is seen an example of an early evolutionary step in the modification of the shape of the teeth in reptiles, for though all are conical they have the appearance of separation into incisors, canines and cheek teeth, by the presence of a pair of tusk-like caniniform teeth, and are suggestive of a first step towards a heterodont dentition. In *Cynognathus* is a pronounced advance, for behind the canine-like teeth are others of a heterodont pattern, the molar crowns being triconodont, with a large central cone, and two small lateral cusps, the dentition appearing almost mammalian.

Pterosauria, or flying reptiles, abounded in the Jurassic and Cretaceous periods of Europe and America. They had a bat-like appearance, from the great expanse of membrane with which they flew, and which was attached to an immensely prolonged finger; they are known as *Pterodactyles*. They varied considerably in size; in some of the largest the membrane was expanded 18 to 25 feet. In many Pterodactyles the jaws were furnished with large pointed compressed teeth, fixed in sockets, while there are other instances as *Pteranodon*, where the jaws were edentulous and probably covered with horn, forming a beak, as in the turtle.

TEETH OF BIRDS

In no living bird is there a trace of teeth, or even tooth germs, although there is now evidence of toothed birds from the Cretaceous rocks of America. The American Geological

Survey, under the leadership of Professor Marsh, recently brought to light startling illustrations in the Cretaceous beds of Kansas of fossil forms of Archaic toothed birds, which in the simple vertebræ, small brains, and jaws armed with numerous teeth, showed many reptilian characteristics.

They are grouped under the class **Odontornithes,** in which are represented—

Odontotormæ. Flying birds, as *Ichthyornis*, having teeth in both jaws, fixed in sockets.

Odontolcæ. Large diving birds, as *Hesperornis*, where the numerous teeth were implanted in grooves, as in Ichthyosaurus, which were replaced in the same manner as in the crocodile by the excavation of their bases, by the succeeding tooth germs, leading to vertical displacement.

Archæopteryx. The oldest specimen of bird hitherto discovered in Europe is Archæopteryx, from the Jurassic rocks of South Germany, about the size of a pigeon.

The fossil shows that it had many reptilian affinities, as the long tail with a pair of feathers arising from each joint, like the tail of a kite, and the jaws furnished with numerous sharp conical teeth, together with a very small brain.

CHAPTER XIII

THE ATTACHMENT OF TEETH

Teeth are attached to the bone by a variety of methods, though most of them may be grouped under four heads.

1. Attachment to a fibrous membrane, as in sharks and rays and dog-fish.

2. Attachment by an elastic hinge, as in the pike, angler, and hake.

3. Attachment by anchylosis, as in the teeth of many fish and reptiles—in sargus, lower teeth of pike, outer teeth of angler and hake, and in the teeth of snakes.

4. Implantation in a socket, as in the teeth of man.

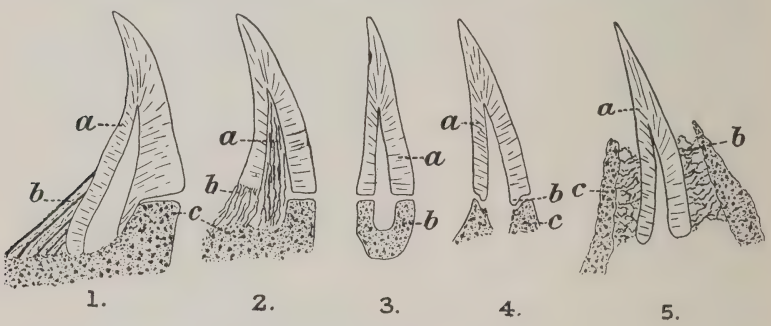


Fig. 192.—Attachment of teeth.

1. Elastic hinge of Angler Fish: *a*, tooth; *b*, elastic hinge; *c*, buttress of bone.
2. Hinged tooth of pike: *a*, elastic fibres; *b*, hinge with non-elastic fibres; *c*, bone.
3. Tooth of eel resting on cylinder of bone: *a*, tooth; *b*, cylinder of bone.
4. Tooth of haddock, partly socketed: *a*, tooth; *b*, prolongation of base into socket; *c*, bone.
5. Tooth of mackerel, slung in groove, to the sides of which it is adherent by coarse bone.

I. **Attachment to a Fibrous Membrane.**—The teeth of sharks, rays and dog-fishes are fixed to a dense fibrous membrane which covers the jaws.

In the shark there are several rows of teeth one behind the other, symmetrically arranged; one row only is upright, on the

surface of the cartilaginous jaw, those behind lie with the points directed downwards and inwards and are concealed under a thick flap of mucous membrane.

Each tooth is embedded in the tough membrane, and attached by strong fibrous bands. The membrane is continually moving upwards, and rotates over the surface of the jaw, carrying its rows of teeth onwards; those occupying the summit of the jaw are lost early, and their places recruited by the never-ending band, proceeding from below.

II. Attachment by an Elastic Hinge.

1. Angler (*Lophius*).—In the capacious mouth of the angler fish the jaws are lined with two rows of strong conical teeth, the outer slightly smaller teeth are anchylosed; the larger, hinder row, hinged. The front of the hinged tooth is free, resting on a buttress of bone, the back is tied down to the jaw by a hinge of fibrous ligaments which spring the tooth into its place, after being bent inwards by the swallowing of prey, when it resumes its normal position.

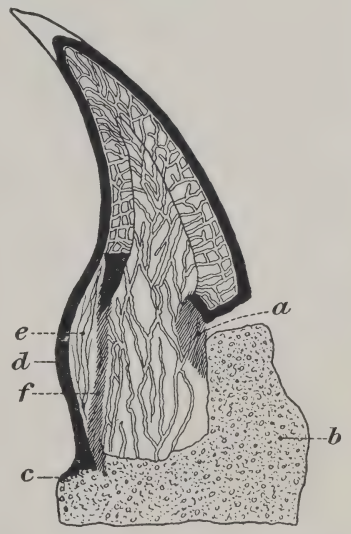


Fig. 193.—Hinged tooth of the Hake (*Merlucius*). (Drawn from Mummery's *Microscopic Anatomy of the Teeth.*)

a, labial fibrous hinge; *b*, buttress of bone; *c*, attachment of lingual portion of main hinge to bone; *d*, semi-calcified matrix continuous with normal vaso-dentine above; *e*, triangular space with scattered fibres; *f*, fibrous portion of main hinge.

2. Hake (*Merlucius*).—The outer row of teeth in either jaw are anchylosed, the inner row being hinged. The teeth are recurved and sharp, and are tipped with a point of so-called enamel. The hinge allows of a bending movement inwards to an angle of 45°, and when the pressure is released ensures their return to the upright position with a snap.

The lingual surface of the teeth is prolonged downwards beyond the limit of the free outer or labial surface to be inserted into the bone. The base of the outer surface is rounded and is received on a raised specially developed buttress of bone.

The elasticity of the hinge was said to be in the partially calcified prolonged lingual portion of the tooth, but Mummery has recently shown that it is a more complex structure than was supposed. In addition to the main lingual hinge he has described a subsidiary hinge attached to the sides of the base of the outer labial edge of the tooth, and the buttress of bone which receives it. It was found after division of the outer hinge that the elasticity of the main hinge was not impaired, but the tooth was less secure on its pedestal and could easily be moved from side to side. This supporting structure is divided into two portions, the tooth in the centre being unattached, so that it is possible here to insert a probe into the pulp chamber. It consists of stout fibres which are attached on the one hand to the tooth and on the other to the bone.

The *lingual hinge* consists of a lingual portion of partly calcified dentine, containing no vascular canals, continuous with the normal vaso-dentine and extending as far as the bone of attachment with which it is incorporated.

On the pulp side of the hinge some coarse fibres are attached to the dentine above and to the partly calcified tissue of the hinge below. These fibres are of about the thickness of elastic fibres, and may possibly be such. In the middle of the hinge, between the partly calcified tissue and the fibrous tissue, there is a triangular space in which some fibres can be seen.

3. Pike (*Esox*).—In the upper jaw of the pike are three bands of small, pointed, recurved teeth, a median and two lateral bands, which cover the palate, and are all hinged.

The hinge consists of fibrous rods, or uncalcified trabeculæ, very elastic in character, fixed to the inner face of the tooth, and shooting downwards through the pulp to the bone below, to which they are tied.

The elasticity is remarkable, for when swallowing, the body of the victim is carried onwards by the bending of the teeth, those in the median line being directed towards the back of the mouth, and those on the lateral bands slanting towards the median line, hence its very struggles only assist its descent into the gullet.

When the body has passed over the teeth, and relieved the pressure, they instantly regain their upright position, preventing the escape of the prey.

Though the back of the hinged tooth of the pike is fixed by a membranous attachment, it is not elastic.

III. **Attachment by Anchylosis.**—There are numerous illustrations of this form of attachment, both in fishes and reptiles. This method can be well studied in the large lower teeth of the pike, or the outer teeth of the angler fish. Each tooth appears to be fused to the bone by an intervening coarse bone, termed the bone of attachment, united to the tooth at its base, and also to the jaw. It is formed by the periosteum, is much coarser in character than bone, the lacunæ more irregular, the lamination marked, and there appears no break in continuity with either the tooth or the bone. It is of a temporary nature, and when a tooth is lost, the bone of attachment is entirely removed by absorption prior to the fixing of another.

Examples are seen in fishes, in the outer row of teeth in the hake, and in the wolf-fish, sargus, and chrysophrys, and also in the pharyngeal teeth of carp.

In reptiles this method is illustrated in the teeth of snakes, as in the python, where the powerful conical teeth are anchylosed, and also in the fangs of venomous snakes.

When one of the poison fangs in a puff adder or rattlesnake is injured or lost rapid absorption of the bone of attachment takes place, removing it entirely, and preparing the surface of the jaw to receive the replacing tooth.

The tooth of the eel rests upon a hollow cylinder of bone of attachment, coarse in character, surmounting the surface of the jaw. This bone is only of a temporary nature, its laminæ take a different direction from those of the jawbone, and when a tooth is lost, the bone of attachment is speedily removed by absorption. The base of the tooth appears to rest upon the summit of the hollow cylinder, in an acrodont fashion, the dentine not blending with the bony structure beneath, and the tooth is easily lost.

In the tooth of haddock the outer part rests on a hollow cylinder of bone like the eel, but the inner side is continued into the hollow cylinder beneath. There is no break in continuity between the tooth pulp and the vessels of the bone of attachment below.

The mackerel's jaw consists of a thin deep groove, to the sides of which the outer part of the teeth are fixed by a coarse

bone of attachment, their bases, widely open, are not resting upon anything.

IV. **Attachment by Implantation in a Socket.**—(Gomphosis.)—This method of attachment exists in all mammals. The teeth are embedded by their roots in sockets, which are moulded to fit them, a vascular membrane intervening, the alveolo-dental periosteum, the source of nourishment to both tooth and socket bone.

The crocodile is an example among reptiles, each conical tooth being fitted into an already existing socket ; and in fishes there are a few instances, as in the rostral teeth of the sawfish (*Pristis*), in lepidosteus, Barracuda pike, sargus, and wrasse.

CHAPTER XIV

HOMOLOGIES OF THE TEETH

Homodont Dentition.—The primitive shape of a tooth is a cone, and teeth of this shape are said to be haplodont. Among fish and reptiles the teeth are usually of the same form in all parts of the mouth, and they are then described as homodont. Such teeth may also be found among mammals; in the Cetacea are examples of teeth of a simple pattern, such as the sharp pointed conical teeth arming the jaws of the dolphin, numbering 200, not differing from one another nor divided into groups. The same characteristic is seen in the porpoise, with its 100 teeth, compressed cones, also the grampus and many whales.

The dentition of Edentates is similar, as is seen in the conical teeth of armadillos and sloths. In the case of suppression of the teeth, as they become functionless, they revert to a conical shape, as in the front premolars of the bear, fruit bat and squirrel, the cheek teeth of the elephant seal, the degraded molars of *Proteles* (aardwolf), and in the changing upper lateral incisors in man, and numerous other examples.

Heterodont Dentition.—In the great majority of mammals the teeth vary in form in different parts of the mouth, and are said to be heterodont. They may be divided into four groups: Incisors, Canines, Premolars and Molars, which occupy different parts of the mouth, varying in pattern, and limited in number. It seems to be a rule, with few exceptions, that a heterodont dentition is usually diphyodont (with two sets of teeth), while a homodont dentition is monophyodont (with one set only).

Number.—The typical Eutherian dentition is represented by the formula: Incisors, $\frac{3-3}{3-3}$; Canines, $\frac{1-1}{1-1}$; Premolars, $\frac{4-4}{4-4}$;

Molars, $\frac{3-3}{3-3}$; total, 44, possessed at the present day by only a few animals, the mole, myogale and gymnura among the Insectivora, and the pig and horse in the Ungulates.

The palæontological record shows that as the ancestry of mammals is traced backwards, the dentition of the early progenitors was generally of a simple character, without a break in the series, no tooth being raised (man only now has that characteristic). The transition in form was gradual, without marked difference. Anoplotherium and Homalodontotherium, primitive Eocene Ungulates, are examples.

Incisors.—The upper incisors are cutting teeth implanted in the intermaxillary bone, and are opposed to similar teeth in the lower jaw. They are single rooted except in the double rooted, outer, upper, incisor of Galæopithecus, and vary in shape in different animals.

Canines.—The upper canine is the first tooth outside the intermaxillary suture; the fourth tooth from the centre in the lower jaw in the architypal dentition is known as the canine, though often now lacking its shape, as in the lower canine of the ruminants, which is flattened and incisor-shaped, and in series with the incisors. Canines are generally stout teeth, with conical pointed crowns, single rooted, though occasionally the human lower canine root is bifurcated. In occlusion the crown of the lower passes in front of the upper canine.

The upper canine of the mole is two rooted, and fixed in the intermaxillary suture, while the lower is small, and in series with the incisors, from which it cannot be distinguished; the tooth doing duty for the canine being the caniniform first premolar. The same is noticeable in the lemur, where the attenuated long canines are in series with the narrow procumbent incisors, while the tooth doing duty for the canine is the enlarged caniniform premolar, which closes *behind* the upper canine, and so reveals its identity.

Premolars.—Behind each canine is a series of cheek teeth, normally seven in number, four premolars and three molars. The premolars have deciduous predecessors, which they vertically displace, though often the first has none. In hyrax, tapir and rhinoceros, however, all are preceded by milk teeth. They somewhat resemble the molars in pattern, but are smaller, though in horse and rhinoceros they equal the molars in size.

Molars have no predecessors, in eruption they follow one another at the back of the mouth behind the deciduous set, as the jaws develop and lengthen.

The form of the molar crown varies according to the habits of the animal, being rendered complex by the upgrowth of the basal ridge, or cingulum, and various tubercles, cusps, or ridges for comminuting the food. Thus in omnivorous animals, as the pig, the crown surface has large rounded nipple-shaped cusps (bunodont), in herbivora such as sheep, tapir and elephant, transverse ridges with deep valleys (lophodont), straight in tapir, curved in rhinoceros, winding in horse ; and in carnivora a sectorial crown for flesh-eating purposes, while in insectivora the surface of the crown is covered with sharp pointed cusps for crushing the shells of beetles and other insects.

The wearing of the crown is a distinct advantage, as the erosion of the surface of the enamel from the cusps exposes the softer dentine and cementum, so that the three tissues being of different degrees of hardness are worn unevenly. More rapid wear of the dentine and cementum leaves the enamel ridges exposed and rough, resembling a millstone condition, well seen in the complex molar of the horse.

Tooth Form.—A tooth is composed of crown, root, and neck, the crown being the portion above the gums and alveoli, the root or roots embedded in bony sockets in the jaw (alveoli), the neck being the junction of crown and root, where the tooth is often constricted. In reptiles the teeth are *always* single rooted. The interior of the tooth is occupied by the *pulp cavity*, containing the pulp or nutrient organ, which supplies the tooth with nourishment and sensation. A tooth may be either *brachyodont* in character, as the molars of the pig, with short broad crowns and long roots, or *hypsodont*, as the molars of the horse or elephant, where the crowns are long and roots short.

The *Alveolo-Dental Membrane* when present, lines the interior of the socket, connecting the roots with the alveoli, and further, clothes and nourishes them, acting as a cushion on which the tooth is slung.

In many of the whales the teeth are only attached in a broad open gutter of the jawbone by means of a dense gum, so that teeth and gum can be stripped away together. In the

extinct saurian Ichthyosaurus the flat-bottomed teeth were ranged one behind the other in the open groove of the jaw, resembling ninepins.

Teeth of Persistent Growth.—Usually when the tooth is fully formed only a small foramen remains open at the end of each root for the passage of the vessels and nerves into the canal leading up to the central pulp chamber, but in some instances the roots remain widely open at the ends to accommodate the large formative pulps, constantly supplying materials for the rapidly growing tusks, as in the elephant, boar and hippopotamus. Such teeth are described as having *persistent* pulps. Examples are seen in incisors, canines and molars, e.g.—

Incisors.—In the persistent incisor tusks of hippopotamus, tusks of narwal, dugong and elephant, incisor teeth of rodents.

Canines.—Tusks of boar, musk deer, walrus, though in old age the ends of the roots of the latter close.

Molars.—In the molars of rabbit, capypara and wombat.

A survey of the dentition of modern animals, especially mammals, shows us distinctly the traces of evolutionary progress by means of the teeth.

Suppression of some teeth and specialization of others is very evident. In some cases, as in the Baleen whale, their entire disappearance has been an advantage, being replaced by the creation of the complex and efficient strainer, for entangling the small mollusca and pteropods in masses, which now form its food. The whale no longer requires individual teeth to catch a fish at a time, and the evidence of the former existence of teeth is only now found *in utero*.

Teeth have disappeared in different animals in all parts of the series. In the incisor region this is very marked, as in the Ruminants, where the entire series of upper incisor teeth, together with the upper canines, have been suppressed, and the sheep now tears the herbage with the procumbent lower incisors and canines impinging on a pad of dense hard gum in the upper jaw.

Stages in the evolutionary progress are seen in the camel, where the third upper incisors and canines are still retained, while in the musk deer, though the upper incisors have all disappeared, the canines remain.

The rabbit and hare are extraordinarily interesting illus-

trations, for the tiny pair of functionless teeth, tucked behind the upper scalpriform incisors, eloquently proclaim the story of the Rodent evolution, the enlarging and specializing of one pair of incisors, the gradual reduction in size of the two other pairs, the lengthening and narrowing of the jaws have crowded out the small functionless teeth, until in the typical Rodent only the powerful chisel-shaped teeth now remain, a most efficient apparatus for the needs of the animal. The small useless teeth in the rabbit are the last links of the chain.

Canines are entirely absent in the kangaroos and wombat among marsupials, and among Eutherian mammals in manatee, hyrax, elephant and rodents.

The Evolution of Compound Molars

The law of trituberculy was suggested by Professor Cope as a result of the discovery of remains of Eocene mammals in New Mexico.

It has been investigated by scientists all over the world, and numerous books and papers have been written confirming or opposing his views. The majority of American scientists are in agreement with the theory, and Professor Osborn has gathered together the evidence for and against.

In reference to the discovery of the extremely ancient forms from the lower Eocene beds of New Mexico, he states : " These small strange fossil mammals exhibited a general similarity in all the molar or grinding teeth, even in animals which had great diversity of feeding habits." " This similarity consisted in the possession of three main tubercles, on the crowns of both upper and lower molars, disposed in triangles."

This was evidently a primitive type of molar tooth, and in 1883 Professor Cope appropriately named it the tritubercular type ; and by comparison with the teeth of more recent mammals the further conclusion was reached that the tritubercular type was ancestral to many, if not to all, of the higher types of molar teeth. Professor Cope thought that the tritubercular type developed during the long Mesozoic period from an ancestral reptilian tooth, consisting only of a single cone, to which was subsequently added a pair of lateral denticles in the following stages :

1. A simple cone interlocking in closure with that of the lower jaw (haplodont).

2. A cone to which lateral conules have been added (triconodont). Examples of this kind have been found in Dromatherium and Triconodon, from the American Trias, and Triconodon from the English Cretaceous rocks.

These primitive animals show the typical heterodont dentition of mammals, with the teeth divided into incisors, canines, premolars and molars, and the lower jaw consists of a single bone, thus distinguishing it from that of a reptile.

3. The lateral conules become enlarged into tubercles, and the crown becomes triangular in shape with a tritubercular

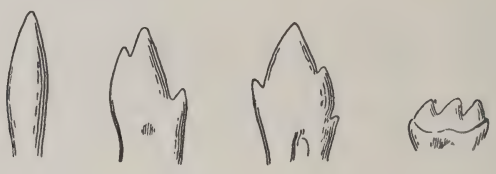


FIG. 194.—1. Haplodont; 2. protodont; 3. protodont with accessory cusp; 4. triconodont (after Osborn).

apex (tritubercular tooth). In the upper jaw, the apex of the triangle, the protocone is internal, and the two outer tubercles are known as the paracone (anterior) and metacone (posterior). In the lower jaw the position is reversed, and for convenience of description the cones are called conids, to distinguish them from those of the upper jaw. Thus the protoconid is external, and the paraconid and metaconid internal. It should be noted that the tritubercular teeth, of which so many fossil remains exist, still interdigitate with those of the opposing jaw.

4. Professor Osborn considers that the Tritubercular tooth is undoubtedly the ancestral molar type of the primates, carnivora, ungulata, chiroptera, and of several, if not all, of the marsupials, and explains the affinities of the complex molar forms found in these orders—which no longer interdigitate, but meet in direct occlusion—with the interdigitating teeth of the primitive tritubercular pattern, somewhat as follows. A spur or talon arises in the distal portion of the crown, which ultimately comes to bear a fourth cone, the hypocone (upper)

or hypoconid (lower). Other minor cusps also appear on the talon called conules, or conulids, so that Professor Osborn says, "In the lower Eocene mammals the lower molar generally bore six cusps: the protoconid, paraconid, and metaconid, in the trigon and the hypocone, hypoconulid, and entaconulid on the talon. . . . It was thus ready for transformation into the molar of a primate, an ungulate, or a carnivore, as the case might be." Such conversion might involve the suppression of one of the cusps of the primitive triangle, for example, the metaconid in carnivora, and paraconid in ungulata. For even in dentitions with a continuous occlusal molar surface, like those of the horse and man, the primitive trigons always interdigitate, each meeting in occlusion the talon of the opposing tooth and its supplementary cusps, never the corresponding trigon. A tooth in which the talon and its cusps is developed is called the tritubercular sectorial tooth, and is common in early mammals."

Against this elaborate theory there are numerous objections. The geological evidence of tritubercular teeth amongst early mammals, though striking, is far from complete, and multitubercular teeth are found in the earliest mammals. Further, embryology shows that in upper molars the paracone is developed before the protocone, though if the latter were more primitive, we should expect it to appear first. At the same time Professor Osborn points out that "the almost universal predominance of trituberculy in the early geological periods is very significant of the uniformity of the molar origin, for of twenty known Mesozoic genera (of mammals), all except three show tuberculy in some of its stages," and in the lower American Eocene rocks, out of eighty-two species, only four had quadritubercular molars; all the others were tritubercular.

Professor Osborn further claims that in the teeth of many succeeding, as well as existing mammals, trituberculy is evident. In the Metatheria the opossum (*Didelphys*) and marsupial mole (*Notoryctes*) have tritubercular molars, and in the Insectivora the tenrec (*Centetes*) of Madagascar, and the golden mole (*Chrysochloris*) are similar examples.

In the Cetacea the molars of the extinct zeuglodon were flattened cones, consisting of a large central cone, and on either side three lateral cones, and this order furnishes examples of

the first stage of tritubercuIy in the haplodont dentition of dolphin, e.g. the triconodont dentition of leopard seal.

In the Creodonta from the basal Eocene, an order of animals closely allied to the Carnivora, the molars are distinctly tritubercular, and among modern Carnivora the crowns of some teeth may show evidence of a tritubercular origin.

The Primates are no exception to this rule, for Anaptomorphus of the Lower Eocene, and the modern Tarsius of Eastern Asia, have identical tricuspid molars, as have also the lemurs of Madagascar. From such a primitive pattern the molars of anthropoid apes and man have probably evolved.

But in spite of this evidence the tritubercular theory finds less adherents than formerly, and though it elucidates the evolution of some tooth forms, is certainly of less general application than its propounders believed. Applying it to man's dentition we find the upper and lower molars to be built up as follows—

Upper Molars :

Antero internal	cusp.	Protocone, *pr.*
Postero ,,	,,	Hypocone, *hy.*
Antero external	,,	Paracone, *pa.*
Postero ,,	,,	Metacone, *me.*

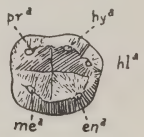


Fig. 195.

Lower Molars :

Antero external	cusp.	Protoconid, pr^d.
Postero ,,	,,	Hypoconid, hy^d.
Antero internal	,,	Metaconid, me^d.
Postero ,,	,,	Entoconid, en^d.
Postero mesial	,,	Hypoconulid, hl^d.

It is evident that man's first upper molar has attained its present quadritubercular form by the up-growth of a spur on the distal surface of the crown which, gradually rising and enlarging, has converted the primitive tritubercular tooth into its present human form. In the higher races the second and third upper molars often clearly tell the story of the molar evolution, as being restricted in room by the present limited accommodation in the jaws; they revert in type to the primitive tricuspid pattern, both the protocone and hypocone becoming fused into one lingual cusp.

In the Eskimo race the hypocone is generally absent in the molars, and the dentition is an example of reversion to a primitive tritubercular type.

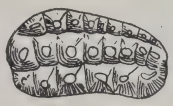


Fig. 196.—Multitubercular molar of Ptilodus, a Mesozoic Mammal (Osborn).

"In the human molar" Professor Osborn suggests "that every component tubercle has its pedigree, and it can be demonstrated almost beyond a doubt which of these tubercles is homologous with the single reptilian cone."

In opposition to the tritubercular theory Dr. Carl Röse, of Freiburg, and others, have suggested a different origin for the mammalian molars, the **theory of concrescence.**

Starting on the assumption that the farther back the evolution of the molars is traced, the simpler and more numerous they become, until ultimately the single rooted primitive cone is reached, as in the armadillo (*Priodon*) with its 100 conical teeth, or the dolphin, with a haplodont dentition of 200 teeth.

He suggests that these numerous cones arranged in a line became grouped together, and were ultimately fused into the complex molars existing at the present, the cusps representing the individual cones.

Against this assumption there are the complex molars of the elephant, which can be clearly traced evolving from a bunodont, pig-like molar, enlarged into a compound, hypsodont molar; or the third molar of the wart hog, which has assumed its great size and hypsodont character by reason of the abnor-

mal growth of the canines, crowding out the anterior teeth, a characteristic of comparatively late occurrence.

There are moreover examples of accessory cusps from the rising of the cingulum, in the molars of the Insectivora, and those of Ruminants, as well as occasionally in the human first upper molar, where an additional lingual cusp is present in both the deciduous and permanent teeth ; it is more often observed in the higher than the lower races of mankind.

Another strong objection to the tritubercular theory is that from the same exceedingly remote geological epoch, which gave rise in America to the triconodont forms of Triassic

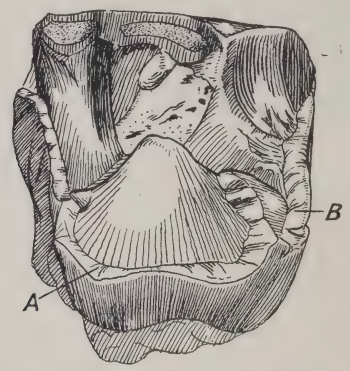


Fig. 197.—Upper Molar of Titanotherium with enlarged Cingulum (A and B).

mammals, there is found in the Trias of England and Germany, Microlestes, a mammal with a molar of quite opposite character. It has a broad saucer-shaped crown, with a crenulated margin, and a somewhat similar instance is Tritylodon, a small mammal from the Trias of South Africa, with square molars, whose crowns were of multituberculate pattern.

The Multituberculates increased during the Jurassic and Cretaceous periods, the molars became more complex from the multiplication of the tubercles, and these forms were continued to the base of the Eocene.

The fact remains that the tritubercular and multitubercular forms appeared in the same very early period, and existed side by side through the Trias, Jurassic and Cretaceous periods, right up to the dawn of the Eocene. The molars of the multituberculates were apparently derived independently from the

simple reptilian cone, hence the supposition follows that the tritubercular type represents but one of several ways in which the complex molars of different groups have been derived, and that no theory involving an absolute uniformity of succession in the development of complete molars will hold true for all groups of mammals.

Cingulum Theory.—Marett Tims strongly urges the importance of the cingulum, or basal ridge, a ring of enamel encircling the crown of a tooth at its base, as a factor in the formation of the tooth crown and its cusps, to which suggestion the authors agree.

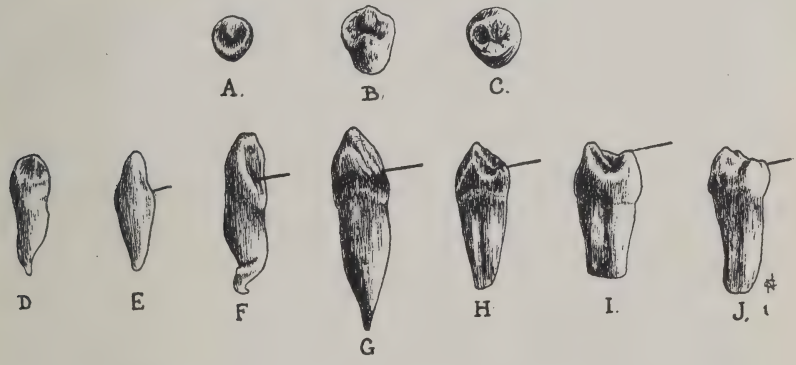


Fig. 198.—Influence of Cingulum in Cusp Formation.

A, crown of first lower bicuspid; *B*, crown of first upper bicuspid; *C*, crown of second lower bicuspid; *D*, conical supernumerary tooth; *E*, stunted upper lateral incisor; *F*, normal upper lateral incisor; *G*, upper canine; *H*, first lower premolar; *I*, first upper premolar; *J*, second lower premolar.

The cingulum undoubtedly plays a most important part, and considerably modifies the tooth form by the elevation of additional cusps, which frequently disguise the original primitive pattern.

An example of the commencement of such a process is seen in the rounded teeth of the porpoise; on the compressed inner surface a small lingual cusp is occasionally formed in a tooth by the raising of the cingulum.

In the unworn premolar of Titanotherium, Fig. 197, an extinct Ungulate allied to the rhinoceros, the cingulum stands as an elevated embracing ring around the crown, and is a notable feature, suggesting possibilities in the modification

of the occlusal surface. This is also seen in the upper molar of rhinoceros, Fig. 220, and in mastodon, Fig. 225.

In the hedgehog, the original quadricuspid upper molars have an additional upper cusp formed by the basal ridge, while the molars of the mole bristle with additional cusps, from the same source.

The influence of the cingulum on the anterior human teeth is suggested in Figure 198, where its modification is apparent on the lingual surfaces. *D* is a small conical supernumerary tooth ; *E* is a stunted upper lateral incisor with the cingulum only just apparent ; in *F*, a normal upper lateral incisor, considerable development has formed a small cusp ; in the upper canine, *G*, the lingual surface is quite cusp-like ; in *H*, a first lower premolar, the cusp is raised still further, but small in comparison with the buccal cusp ; while in *I*, the first upper premolar, the two cusps are almost of equal length, and in *J*, the second lower premolar, the cingulum is raised mesially and distally to form a quadricuspid crown. The effect is seen in human molars where, occasionally, additional cusps are formed by the same means both in the temporary and permanent dentitions.

Milk Dentition

In the Mammalia the permanent dentition is usually preceded by milk or deciduous teeth. Among them it seems to be a rule with but few exceptions that when teeth are homodont, only one set is produced (monophyodont), but when the crowns are heterodont, differing in pattern, they are diphyodont, that is they have deciduous and permanent teeth. There are exceptions, however, for though the sloths and armadillos, with simple conical teeth, are homodont and monophyodont, yet the nine-banded armadillo (*Tatusia peba*) is diphyodont.

Likewise Orycteropus, the ant-eater of the Cape, has functionless cheek teeth $\frac{7}{4}$ on each side, the last tooth molariform with two roots, indicating different habits in past ages.

The rat has no deciduous teeth, and therefore is an exception to the diphyodont rule.

The homodont, monophyodont dentition of the Cetaceans is

regarded as the milk set, while the single persistent dentition seen in many Edentates is the permanent set.

The milk teeth may be functional and retained for some considerable time, as in the deciduous teeth in the Ungulates exemplified by the pig, sheep, horse and tapir, where they are in use until the animal is fully grown, and resemble their permanent successors. Taking the pig as an example, the milk teeth number i. $\frac{3}{3}$, c. $\frac{1}{1}$, mm. $\frac{3}{3}$, total 28. In Proboscidea (elephant, mastodon, and dinotherium) the milk molars are large and functional, and the elephant also has deciduous tusks.

In the Carnivora well-developed milk teeth exist in the great majority of animals, numbering i. $\frac{3}{3}$, c. $\frac{1}{1}$ mm., $\frac{3}{3}$, total 28, except in Felidæ, where the molars number mm. $\frac{3}{2}$. The Aquatic Carnivora have quite a rudimentary deciduous set, as in the seal, where they are functionless and shed before birth.

In the Primates, the monkeys and man possess a milk set numbering i. $\frac{2}{2}$, c. $\frac{1}{1}$, mm. $\frac{2}{2}$, total 20, which in man are retained for many years, the last milk molars being lost about the 9th or 10th year.

On the other hand we find numerous instances where the milk teeth are functionless, as in the tooth germs found in the gutter of the jaws of the whalebone whale, which never erupt, but are absorbed *in utero*, or in the simple conical deciduous teeth of the mole, i. $\frac{3}{3}$, c. $\frac{1}{1}$, mm. $\frac{4}{4}$, total 32, which disappear about the time of birth, or in the minute conical milk teeth of the bat.

In the Rodents they vary considerably, the mm. $\frac{1}{1}$ being lost *in utero* in the guineapig.

In hares and rabbits the milk dentition numbers i. $\frac{2}{1}$, mm. $\frac{3}{2}$ $=16$, and is lost about the eighteenth day after birth, but the mm. $\frac{1}{1}$ of the beaver are retained for a long time. In Marsupials the deciduous teeth are reduced to one molar on each side of each jaw, a characteristic also seen in Triconodon, a small Mesozoic primitive mammal.

It is now generally considered that the early dentition of mammals was that of diphyodontism.

Usually the hindmost milk molar resembles the first permanent milk molar in pattern, this being well seen in the Ungulates, Carnivora, and the Primates. The second milk

molar in man has all the characteristics of the permanent teeth, including the oblique ridge.

Milk molars are displaced vertically by the permanent premolars. As the former erupt, their roots are wide and divergent to accommodate the developing crowns of their successors.

TERTIARY PERIOD. AGE OF MAMMALS

Chart of the subdivision of the Tertiary (Cainozoic) and Quaternary Periods

Recent.	Represented by the present animals and man.
Pleistocene. (Gr. *pleistos*, most *kainos*, new)	Represented largely by the Ice Age, when man and modern animals appeared.
Pliocene. (Gr. *pleiōn*, more *kainos*, new)	Appearance of elephants, hippopotami, camels, giraffes, gazelles, antelopes, wolves, hyænas, porcupines.
Miocene. (Gr. *meiōn*, less, *kainos*, new)	Platyrrhine monkeys in S. America. Catarrhine monkeys and anthropoid apes in Europe, mastodons, tapirs, whales, beavers, deer, chevrotains, seals, otters, bears, dogs, foxes, weasels.
Oligocene. (Gr. *oligos*, small, *kainos*, new.) Short period.	Ancestors of elephants, small primitive monkeys, Parapithecus, and Propliopithecus.
Eocene. (Gr. *ēōs*, dawn, *kainos*, new.) Dawn period. Lower division of the Tertiary.	Earliest mammals, with small brains, but already showing distinctions representing existing natural orders of Primates, Insectivora, Carnivora and Rodents; and Archaic forms which gave rise to the Ungulates, including the ancestors of the horse; Creodonts, progenitors of the Carnivora; Titanotherium, precursors of rhinoceros; and early lemurs.

THE TEETH OF MAMMALIA

CHAPTER XV

PROTOTHERIA AND MARSUPIALIA

Huxley divided mammals, or warm-blooded animals, into three sub-classes.

Sub-Class I.—Prototheria or Monotremata, represented by the duck-billed platypus, echidna or spiny ant-eater, and Proechidna.

Sub-Class II.—Metatheria or Marsupialia, the Marsupials or pouched mammals such as kangaroos, opossums, and wombats.

Sub-Class III.—Eutheria or Placentalia, to which the great majority of existing mammals belong.

Sub-Class I. **Prototheria**

Three existing animals only belong to this sub-class, the Platypus (*Ornithorhyncus anatinus*), Spiny Ant-eater (*Echidna aculeata*) and Proechidna, all inhabitants of Australia. They belong to an old and primitive form of mammalian life, possessing many characteristics absolutely reptilian, and their blood is less warm than that of other mammals.

Platypus is an egg-laying amphibious animal, inhabiting the rivers and lakes of Eastern Australia and Tasmania. It makes long burrows in the river banks, at the extremity of which the nest is found. The body of the platypus is about 18 inches long, covered with soft brown fur, the tail is broad, and flattened for an aquatic life, the feet are webbed, like those of a duck, and the jaws are prolonged into hornlike bills, also resembling those of a duck; to this it owes its name.

Little was known about the platypus until 1884, when Mr. W. H. Caldwell went over to Australia to study its habits, and he found that the female carried in a temporary pouch two eggs, each about $\frac{3}{4}$ of an inch long and covered by a thin white

shell. These were hatched and the young subsequently suckled by the mother.

The internal structure of the creature, together with the egg-laying characteristic, point to the platypus as not only the lowest of mammals, but also one possessing many reptilian affinities. Formerly the platypus was considered to be an example of a mammal with horny teeth, as only a few adult specimens had reached Europe, but shortly after Mr. Caldwell's discovery some very young animals were sent to England, which enabled Mr. Oldfield Thomas to demonstrate that in early life the platypus possesses a dentition of twelve truly calcified teeth, three on each side, in the back of the jaws.

The pattern of the crown of the upper molar is most unusual, unlike that of any existing mammal, being broad and saucer-

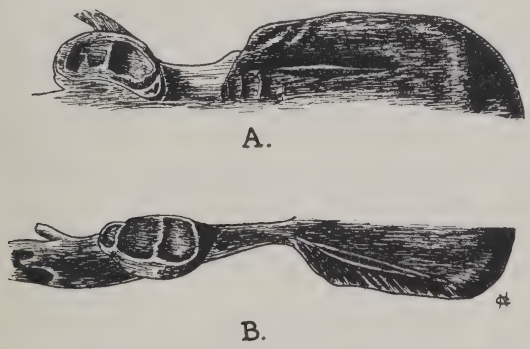


Fig. 199.—Halves of jaws of Platypus.
A, Upper jaw; B, Lower jaw.

shaped with crenulated margins, and with two large internal conical cusps; in the lower jaw the pattern is reversed, the two conical cusps being external. The teeth of the platypus resemble most the fossil teeth of Microlestes, a tiny little creature, which made its appearance in the Trias early in the age of the great reptiles, and it is now generally considered that the duckbill approximates to these extremely ancient forms, and represents the survival of ancient beasts which lived and flourished myriads of years ago. It stands at the very foot of the ladder of mammalian life, linking together reptiles and mammals.

Structure.—The crown of the tooth is built up of coarse

dentine permeated with interglobular spaces, and the large cusps contain some vascular canals. The roots are diminutive, and occupy shallow crypts. The crowns are subjected to great attrition from the nature of the food of the platypus, which consists of grubs and worms from the river mud. These are mixed up with sand and grit, and effect the rapid wearing away of the crowns, which are speedily lost. In the meantime a growth of oral epithelium dipping down into the alveolar cavities occupies the sockets, fitting like a cushion, under and around the eroded crowns ; and when the remains of the teeth are shed, this epithelium fills up the crypts and cornifies, performing the work of mastication in the adult stage.

Echidna (Spiny Ant-eater) and *Proechidna*, the only other examples of this sub-class, are edentulous. Their food consists of ants, and their habits are similar to those of the ordinary ant-eaters. The body is covered with fur mixed with sharp pointed spines.

Sub-Class II. **Metatheria or Marsupialia**

The sub-class Metatheria, or Marsupialia, is confined principally to the continent of Australia, a few Marsupials being found in New Guinea, the opossum on the North American Continent, and Cœnolestes (a mouse-like animal) in South America.

Though so limited at present, they existed in the other continents in Mesozoic times, when they were contemporaneous with the great reptiles, their greater intelligence preserving them from destruction. For immense ages, since the end of the Secondary epoch, Australia has been separated by deep seas from the rest of the world ; the animals, which are practically all Marsupials, have been thus protected from the competition of the various orders found in the other continents, where the primitive Marsupials have disappeared and have been superseded by the Eutherian stock, with bigger and more specialized brains. Marsupials have no placenta, and the young are born in a very immature condition, and transferred to the marsupium, or pouch of the mother, where they attach themselves to a mammary fold, or nipple, from which they are suckled and sheltered until fully developed. They represent an intermediate form between the Prototheria on

the one hand, and Eutheria on the other, their small brains more closely resembling the Platypus.

They have separated into groups and families, similar to the higher mammals, being differentiated into insectivorous, herbivorous, carnivorous and rodent-like forms.

General Characteristics of Teeth of Marsupials

1. *Number of Teeth.*—In all Marsupials except the wombat the upper incisors exceed the lower.

Whereas in Eutheria the typical dentition is represented as i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3}$, total 44, in Marsupials the typical formula is i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{4}{4}$, total 44.

2. *Form.*—The teeth approximate in pattern to those of the same habits in the mammals, thus the carnivorous Thylacine has a dentition which somewhat resembles the dog, the insectivorous Myrmecobius mimics the mole, and the herbivorous kangaroo has ridged molars.

3. *Structure.*—The teeth are formed of ortho-dentine, covered with enamel, which has the peculiarity of being penetrated by tubes from the dentine, with the exception of the wombat. The roots are covered with cementum.

4. *Succession.*

Only one premolar has a predecessor, the milk dentition being thus mm. $\frac{1-1}{1-1}$.

This tooth varies considerably in development. In the Thylacine it is calcified, but is absorbed or shed before any other teeth are erupted; in the wombat there is no succession, so that the functional tooth may be a premolar or a molar. In the kangaroos it is present until displaced by the third premolar, which has a crown so large that it vertically displaces both the milk molar and the second premolar.

Another theory regards the replacing tooth as the only permanent tooth, the rest of the functional set being considered milk teeth. This view is supported by many authorities, but recent investigations have thrown new light on this puzzling dentition.

The germ of a missing premolar was found by Marett Tims in the developing tooth of the wallaby, attached to a very long neck of the enamel organ, and crowded down into the submucous tissue. This was considered to be the second premolar, making the cheek teeth p. $\frac{4}{4}$, m, $\frac{4}{4}$. Some observers

refuse the arbitrary division into premolars and molars, and group the side teeth into one class of cheek teeth only: the typical marsupial dental formula thus comes to resemble placental mammals.

5. *Jaws.*—The angle of the lower jaw is inflected in all the Marsupials except Tarsipes; in the kangaroo the two halves of the mandible separate slightly in eating.

6. *Function.*—Polyprotodonts mainly carnivorous, or insectivorous; Diprotodonts mainly herbivorous.

Marsupialia are divided into the orders Polyprotodontia and Diprotodontia.

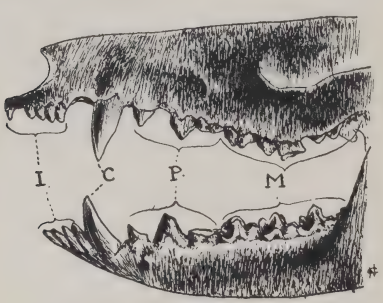


Fig. 200.—Opossum (*Didelphys*).

In *Polyprotodontia* the incisors are numerous, canines developed, and the molars have sharp points on the crowns. The animals representing it are more or less carnivorous or insectivorous, as dasyurus opossums, myrmecobius and bandicoots.

In *Diprotodontia* the dentition somewhat resembles that of a rodent, the central pair of lower incisors becoming enlarged, while the remaining incisors, as well as the canines, are rudimentary and functionless, and tend to disappear. Hence the name given to this order (*di* = two, *prot* = front, *odont* = teeth). In one instance, the wombat, a veritable rodent-like dentition has been produced. Most of the animals in this order are more or less herbivorous. It is interesting to observe that the rodent form has arisen independently from three entirely different stocks, the wombat from the Australian Marsupials, the aye-aye (*Cheiromys*) of Madagascar from a lemurine source, and the rodents of the old world from quite a different origin.

In the Australian Diprotodonts it is easy to mark the various stages in the rodent-like evolution by the gradual enlargement of a pair of incisors, and the suppression of the others, together with the canines.

Sub-Order Polyprotodontia

The *Opossums* (*Didelphys*) are now confined to the continent

of America, but they existed in Europe in the Eocene. They are carnivorous and insectivorous. Some of the opossums in Brazil resemble shrews in size and structure. The dentition is i. $\frac{5}{4}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{4}{4}$, total 50. The canines are long, the molars covered with sharp points, indicating an insectivorous origin. In parts of South America they are almost entirely insectivorous in their habits.

The third premolar is preceded by a milk molar which remains in place until the animal is fully developed. The canines are large, incisors small, and the molars have numerous small cusps on the crowns.

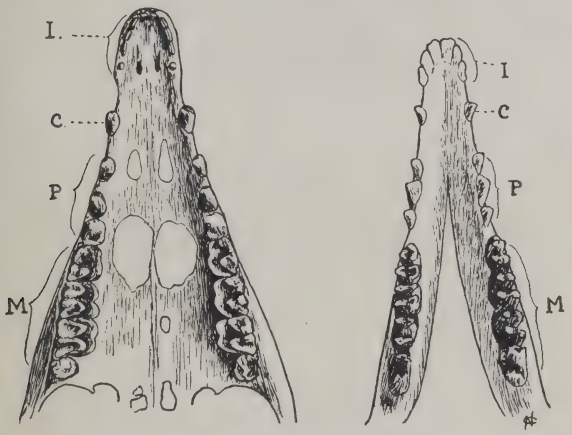


Fig. 201.—Bandicoot (*Parameles*).

Family Dasyuridæ.—The *Thylacine* (*Thylacinus*), with a dentition i. $\frac{4}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{4}{4}$, total 46, is a wolf-like creature now inhabiting Tasmania. It was formerly distributed over the continent of Australia, where numerous remains exist in caves on the mainland.

It is a fierce carnivorous creature, smaller than a wolf, with a dentition which at first sight resembles the dog or wolf, but the numerous incisors proclaim its origin. The outer incisors are largest, the canines long and powerful, the laterally compressed premolars are separated by interspaces as in the fox, interlocking in closure as in the Cape hunting dog, and the molars have pointed cusps as in the Insectivora.

Myrmecobius.—Dentition i. $\frac{4}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{5}{5}$ or $\frac{6}{6}$, total 50

or 54. This is a little creature the size of a squirrel inhabiting Southern and Western Australia, and possesses the largest number of teeth of any existing Marsupial; it is insectivorous in its habits, feeding on ants.

Bandicoot (*Parameles*).—Dentition i. $\frac{4-5}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{4}{4}$, total 46 or 48. The small teeth bristling with cusps appear to resemble the dentition of the mole, its diet being similar, and the last premolar is preceded by a small milk molar, which remains in place for some time.

Sub-Order Diprotodontia

The *Wombats* (*Phascolomys*), of which there are three species living in Australia, are small noctural herbivorous animals of a bear-like appearance. The dentition is i. $\frac{1}{1}$, c. $\frac{0}{0}$, m. $\frac{4}{4}$, total 20. The wombat is an aberrant marsupial form in which the dentition is rodent-like; in the course of its evolution a pair of incisors in each jaw have become enlarged, growing from persistent pulps, and have assumed the curved and scalpriform appearance found in typical rodents. All the remaining incisors, canines and three premolars have disappeared. The molars likewise grow from persistent pulps, being curved and grooved externally, dividing each tooth into two columns. Enamel covers the front of the incisors, while cementum encircles the tooth, thus differing from true rodents. The enamel is unlike all other marsupial enamels in that it is not penetrated by tubes from the dentine.

Koala (*Phascolarctos cinereus*).—Dentition i. $\frac{3}{1}$, c. $\frac{1}{0}$, p. $\frac{1}{1}$, m. $\frac{4}{4}$, total 30. The phalangers are small arboreal animals, nocturnal in their habits, feeding principally upon vegetation. Koala is known as the native bear in Australia, and subsists largely upon the young shoots of eucalyptus.

In this animal is noticeable a stage towards a rodent-like dentition, but the condyles of the mandible are transverse, the central upper incisors are enlarged, and oppose two large procumbent lower incisors, the two remaining pairs of upper incisors are rudimentary and functionless. Behind the central lower persistent incisors is a wide space devoid of teeth, the other incisors and canines having been suppressed. The square

molars have sharp ridged crescentic-shaped cusps, and form with the premolars a continuous series. The milk molar is minute and functionless.

Tarsipes, a small mouse-like creature which feeds on honey and insects, belongs to this family. It is singular in having no inflection of the mandible. Its molars are rudimentary and lost early, but it retains the procumbent lower incisors.

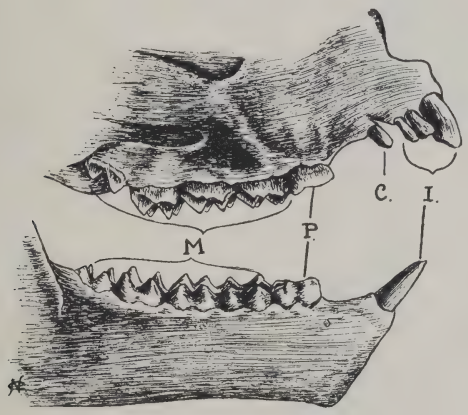


Fig. 202.—Koala (*Phascolarctos cinereus*).

Other examples are the grey cuscus (*Phalanger orientalis*), and the flying phalanger (*Petaurus*).

Kangaroos and *Kangaroo rats* are herbivorous. Dentition i. $\frac{3}{1}$, c. $\frac{0}{0}$, p. $\frac{2}{2}$, m. $\frac{4}{4}$, total 32 (Fig. 203).

In the lower jaw of the Kangaroo (*Macropus*) the only remaining pair of incisors are enlarged, grow from persistent pulps, are procumbent, flattened from side to side on the lingual surface and convex on the outer. When feeding the teeth have a curious scissors-like action, from the two halves of the mandible being loose and attached by ligaments only at the symphysis. They are opposed to three pairs of upper incisors, their points being close behind the centrals.

The outer upper incisors, which are the largest, are separated by wide spaces from the premolars, though a minute functionless canine is sometimes present; the molars have transverse ridged crowns (lophodont), which are gradually lost from the front of the series; in the adult the remaining molars gradually

move forwards. The milk molar takes its place in the series, and in consequence of its large crown, displaces the second premolar and the milk molar.

In the kangaroo rat (*Hypsiprymnus*), the third upper premolar is of very large size and uncommon shape, its crown being a trenchant blade with a sharp edge, quite unlike the

Fig. 203.—Kangaroo (*Macropus*).

simple square molar crowns with rounded cusps ; as in the kangaroo, it displaces two teeth. Small canines are present in the upper jaw but absent in the lower.

Extinct Marsupials

In Pleistocene deposits in Australia numerous extinct Marsupial forms have been brought to light, including a gigantic kangaroo (*Macropus Titan*), and an immense wombat as big as a tapir, but these are small in comparison with *Diprotodon*, which equalled the rhinoceros in size, the largest known

Marsupial. It possessed a pair of immense scalpriform incisors in each jaw, growing from persistent pulps ; in the upper jaw two smaller pairs of incisors were present behind the great central pair. Canines were absent, and the molars were ridged.

Thylacoleo, declared by Sir Richard Owen to have been as large as a lion, was once considered to be a gigantic carnivorous

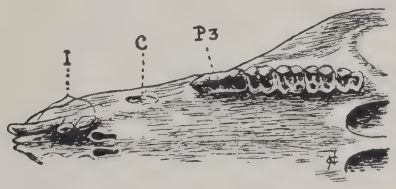


Fig. 204.—Kangaroo rat (*Hypsiprymnus*).

Marsupial, the great size of the thin-edged, blade-like premolar, more than two inches in length, mimicking the carnassial tooth of the lion. It is considered to belong to a family having affinity on the one hand with the Phalangers, and on the other with Macropodidæ, the blade-like premolar of the kangaroo rat having revealed the identity of the carnassial-looking tooth of Thylacoleo : the animal was evidently herbivorous.

It is interesting to note that all the extinct Marsupials of the Old World and America, as well as all that survive outside Australia belong to the order Polyprotodontia. It is thus clear that Diprotodontia is an order that has been evolved in Australia from the original Polyprotodont stock, since that continent became separated from the mainland of Asia.

CHAPTER XVI

EUTHERIA

Orders Edentata, Sirenia, Cetacea

Order Edentata.—Edentates embrace the sloths, armadillos and ant-eaters of Central and South America, and the pangolins and aardvarks of the Old World.

Characteristics of the dentition of Edentata.

1. *Situation.*—Teeth are absent from the premaxilla except in some armadillos, where the anterior tooth is in the premaxilla. The front part of the lower jaw is also destitute of teeth.

2. *Number.*—Variable. In sloths there are usually $\frac{5}{4}$ teeth on each side; in armadillos the teeth are numerous, usually $\frac{8}{9}$ on each side of the jaws; and the dentition of Priodon numbers 100, the teeth gradually falling out from the front of the series. The ant-eaters are edentulous, with one exception, Orycteropus, whose food is similar, and whose mouth is modified for ant eating, yet still possesses permanent teeth, numbering in the adult $\frac{5-5}{5-5}$.

3. *Form.*—Conical, or sub-compressed cones, or cylindrical; homodont and monophyodont, except in the armadillo (*Tatusia peba*) and orycteropus, which have milk teeth.

4. *Structure.*—The teeth are formed of dentine, the axial portion of the pulps being often converted into vaso-dentine; the dentine and cementum of the extinct Megatherium were permeated with vascular loops.

A characteristic of the Edentata is the entire absence of enamel, the teeth consisting of dentine and cementum.

5. *Attachment.*—Being simple cones the teeth are not

divided into crown, root and neck; they are persistent in growth and wear rapidly on the masticating surfaces, interdigitating like the teeth of a saw.

6. *Jaws.*—The jaws are long, narrow and slender in the armadillos, and the mouth is a small aperture, through which the long, slender tongue, covered with viscid saliva, is thrust into the nests of ants. The jaws are shortened for a vegetable diet in the sloths, attenuated in the ant-eaters.

7. *Function.*—The food of armadillos consists of insects, carrion, small snakes, etc.; sloths feed on tropical vegetation, and ant-eaters on ants and termites.

Three-toed Sloth (*Bradypus*).—The teeth, usually $\frac{5}{4}$ on each side of the mouth, are homodont and cylindrical, and, being unprotected by enamel, each tooth wears on the surface into a cup-shaped depression and none project above the others.

Two-toed Sloth (*Cholœpus*) has a similar dentition, but the anterior tooth is large and caniniform and wears to a bevelled edge, the upper closing over the lower, thus differing from the true canines. A space in each jaw separates them from the hinder teeth. No teeth are on the premaxilla.

The structure is hard dentine, with axial vaso-dentine. Cementum covers the teeth, but the absence of enamel causes rapid wear, and the tissues are recruited by persistent pulps.

South America was originally the home of the giant sloths, *Megatherium* and *Mylodon*, rivalling the elephant in size, which flourished during the Pleistocene epoch, and were contemporary with man; extensive remains have been unearthed in the various river gravels.

The dentition of Megatherium resembled that of modern sloths; the teeth were elongated, grooved, and of persistent growth. The unprotected crowns, devoid of enamel, were rapidly worn into two ridged, or bilophodont, shape, mimicking the crowns of manatee and tapir. The structure is orthodentine with a thin coating of cementum, both tissues are permeated with vascular loops, an unusual occurrence in mammals, where vascular dentine is rarely found.

Ant-eaters inhabit the plains of South America and the *Pangolin* eastern Asia and Africa. Some attain a large size, such as the Great Ant-eater (*Myrmecophaga jubata*), which sometimes measures 4 feet in length and 2 feet in height.

In all, the mouth and jaws are profoundly modified, being

elongated and attenuated, with a whip-like tongue for catching ants, and they are edentulous, with the one exception of the *Aardvark* (*Orycteropus*), the ant-eater of South Africa. Its food and habits are similar to those of other ant-eaters, but it possesses a dentition of about thirty-six teeth, which are never all in place at the same time, the front ones being shed before the hind ones are cut. The crowns are hypsodont and slightly heterodont, and of persistent growth, and are preceded by functionless milk teeth, which, however, are never erupted. The crowns are curiously narrowed half way down into an hour-glass shape. The structure is remarkable, being plici-dentine, closely resembling that of Myliobates. It is formed by numerous parallel branches of pulp, which permeate the crown and give off their systems of inosculating dentinal tubes, presenting in section a complex appearance; it is the only instance of such a tissue in the mammalia, plici-dentine being usually associated with the structure of the teeth of primitive fishes and reptiles. Orycteropus is a puzzle in all ways, and though numbered with the Edentates by reason of its structure, diet and habits, in other respects it stands alone.

Armadillos (*Dasypodidae*) are a class of small animals inhabiting the tropical and temperate parts of South America whose bodies are protected by numerous bands of bony scutes or shields. They have a dentition numbering thirty-four to thirty-eight, but Priodon sometimes has one hundred teeth. The teeth are compressed cones, homodont, that is, alike in pattern, and monophyodont. They grow from persistent pulps and being devoid of enamel wear away speedily, the axial portion forms secondary or osteo-dentine, from the rapid calcification of the pulp. The crowns interdigitate, and thus wear down into a wedge shape resembling the teeth of a saw.

FIG. 205.—Dentition of Armadillo (*Dasypus*).

Usually a homodont dentition is not preceded by milk teeth, as in the majority of Edentates, but the Nine-Banded Armadillo (*Tatusia peba*) is an exception and resembles Orycteropus in that respect, with its few rudimentary and functionless milk teeth.

Order Sirenia.—Sirenia are large aquatic mammals, which inhabit the estuaries of tropical rivers and lagoons and shore lines, where they browse on the marine vegetation. They are represented at the present day by the manatee and dugong. The order is an old one geologically, as the remains of Sirenians are found in Eocene and Miocene strata in Europe and Northern Egypt; the creatures evidently abounded in the seas of that period. They exist now on both sides of the Indian Ocean, the Red Sea, and the shores of Northern Australia, where the dugong frequents the Great Barrier reef. Their fore limbs are modified into paddles, and all traces of the hind limbs have disappeared; they are truly aquatic in their habits, feeding beneath the surface on seaweeds and other marine plants, and they never leave the water.

In *Manatee* (*Manatus*) the intermaxillary bone is prolonged and covered with horny plates, all incisor teeth being absent except in very young animals, where two rudimentary functionless teeth are present in each jaw; these never erupt, being buried beneath the horny places. The lower jaw is also covered in front with horny plates, which antagonize with those in the upper jaw; canines are absent. The molars are very numerous, numbering forty-four, or according to Oldfield Thomas, eighty in number; but all are not in place at the same time, usually $\frac{9-9}{9-9} = 36$ being present. The teeth are lost from the front, and replaced at the back of the series, in the same way as the molars of the elephant; they are bilophodont (two transverse ridges) in pattern, resembling those of the tapir and dinotherium, thus suggesting a relationship with Ungulates; they are three-rooted in the upper, and two-rooted in the lower jaw. The crowns are covered with enamel, in which the prisms are straight, and the dentine is permeated with a system of channels, presenting the appearance of vascular canals, though no blood is present. The crowns are square, and the posterior lower molars have a large tubercle on the hinder surface.

In the *Dugong* (*Halicore*) the front part of the upper jaw is bent almost vertically downwards, opposing the deflected symphysis of the lower jaw.

Two incisor tusks of persistent growth, 6 to 8 inches in length, occupy the intermaxillary bone in the male. They are rodent-like teeth, growing from persistent pulps, and covered on the front and sides only with enamel, the back being coated with cementum; in the female the extremity of the tooth has enamel all round. Their apices project only slightly beyond the sockets. They may be regarded as sexual weapons, as in the female they never erupt, but lie concealed in the alveolus, with their roots closed. In both sexes they are preceded by milk incisors.

The front of the deflected lower jaw is covered during life with a horny plate, beneath which lie concealed the germs of several incisor teeth, which are absorbed early, though the widely-open sockets are present for some time. The molars number $\frac{5-5}{5-5}$ and are cylindrical in shape, except the last molar, which is grooved laterally. In early life the crowns are tuberculated, but in adults the surface is much worn and the teeth are gradually lost from the front of the series, until only $\frac{2}{2}$ remain. Their structure resembles the teeth of Edentata, as enamel is replaced by cementum, and while most of the crown consists of ortho-dentine, the axial portion is vaso-dentine. They also resemble the teeth of Edentata in having no milk predecessors.

Steller's Sea Cow (*Rhytina stelleri*) was formerly a third representative of this order. It was discovered by the naturalist Steller in 1741 on the shores of Behrings Straits, which it frequented in great numbers, but it was exterminated by Russian hunters before the end of the century. It attained a size of almost elephantine proportions, measuring from twenty to twenty-five feet in length, but being quite unprotected it was speedily destroyed. The mouth was edentulous, being furnished only with ridged horny plates.

Order Cetacea.—The order Cetacea includes various aquatic mammals, such as dolphins, porpoises and whales; the latter are divided into two sub-orders, the Toothed Whales or *Odontoceti*, and the Baleen Whales or *Mystacoceti*. The Cetaceans are probably derived from terrestrial, carnivorous ancestors.

Characteristics of the dentition of Cetacea.

1. *Situation.*—In the toothed Cetaceans (*Odontoceti*) the teeth are situated on the premaxilla, maxilla and mandible.

2. *Number.*—The teeth vary in number: in the dolphin, 200; porpoise, 100; grampus, 50; sperm whale, 25 in the lower jaw, none in the upper. In Hyperoodon there are two to four in the front of the lower jaw, in Narwhal one in the premaxilla. The baleen whale is edentulous.

3. *Form.*—In shape they are conical and single rooted, as is seen in the sperm whale and dolphin. The molars of the extinct Zeuglodon were compressed, with serrated, pointed crowns, and two rooted. The male narwhal is provided with a long incisor tusk spirally twisted, as a sexual weapon. In Mesoplodon there are a pair of strange, flat, strap-shaped teeth in the lower jaw, one on either side, which are puzzling to understand, as, being bent inwards, in the upper part of the crown, they are apparently functionless.

4. *Structure.*—Ortho-dentine, osteo-dentine, vaso-dentine and cementum are to be found in this order; the dentine is characterized by the number of interglobular spaces. Enamel is uncommon, but forms the tip of the teeth of the bottle-nosed whale and mesoplodon.

5. *Attachment.*—In the sperm whale the teeth are attached to a fibrous gum in the open groove of the lower jaw, and the gum with the teeth attached can be readily torn away. The tusk in the narwhal occupies a deep socket, and most of the teeth of the dolphin and porpoise are socketed.

6. *Succession.*—The teeth of Cetacea being homodont, are monophyodont. No second set has ever been observed; the functional set is the milk dentition.

7. The *jaws* are of considerable length; in the baleen and sperm whales they are gigantic. Numerous tooth germs occupy the gutter in the developing lower jaw of the whalebone whale, in the fœtus, which never properly calcify, and are early absorbed.

8. *Function.*—The dolphin seizes a fish at a time with its sharp-pointed, serried teeth, the sperm whale tears asunder the bodies of the cuttle-fish, while the edentulous whalebone whale accomplishes the same result, its mouth having been converted into a huge strainer for entangling small marine

animals. The tusk of the narwhal is used for sexual combat.

Primitive Cetaceans appeared early in the Eocene. The present haplodont, homodont dentition of Odontoceti has been arrived at by fitting creatures originally provided with heterodont teeth to an aquatic existence, for which we find the conical teeth of fishes, reptiles such as the crocodile, and mammals such as seals, and sea lions, admirably fitted. The evidence of Zeuglodon and the tooth germs of heterodont form in the whalebone whale confirms this. Therefore we regard the present condition of the Odontoceti as retrograde.

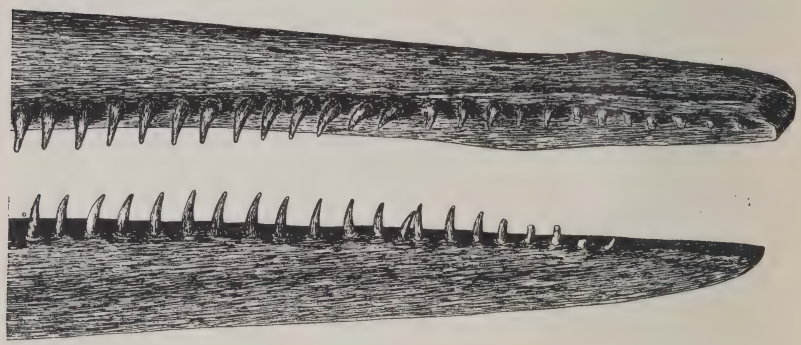


Fig. 206.—Dentition of Dolphin (*Delphinus delphis*).

Odontoceti.—*The Dolphin* (*Delphinus delphis*) is furnished with a dentition of about 200 sharp-pointed, slender, conical teeth.

They interlock in closure and become smaller at both ends of the jaws. At first they are fixed in an open gutter, like Ichthyosaurus, but afterwards the front teeth become socketed by the growth of partitions from the alveolus, while the posterior teeth occupy an alveolar groove. The teeth remain open at the base for a time. In the *Porpoise* (*Phocæna*) the teeth number about 100; they are flattened, compressed cones, with short roots. In the *Grampus* (*Orca*), the teeth are still more limited, numbering from forty to fifty, adapted to the carnivorous habits of this ferocious Cetacean, which attacks and kills seals, and even larger whales, so that it has acquired the popular name of the Killer Whale. The

large teeth are flattened laterally, sharp-pointed, and fixed in deep sockets. In this species the teeth occasionally meet edge to edge, causing rapid attrition, which may result in exposure of the pulp, and an abscess, and subsequent loss of

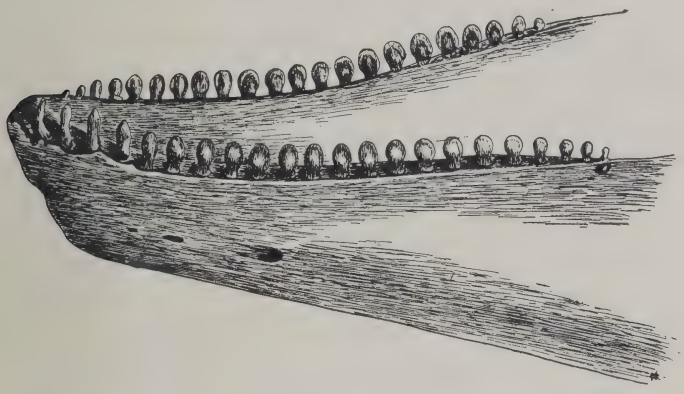


Fig. 207.—Lower jaw of Porpoise (*Phocæna*).

the tooth ; if the wear is less rapid, secondary dentine will be formed.

Toothed Whales.—The sperm whale (*Physeter macrocephalus*) is one of the most colossal animals which has ever existed, measuring from 55 to 60 feet in length. It frequents tropical and subtropical seas, subsisting largely on

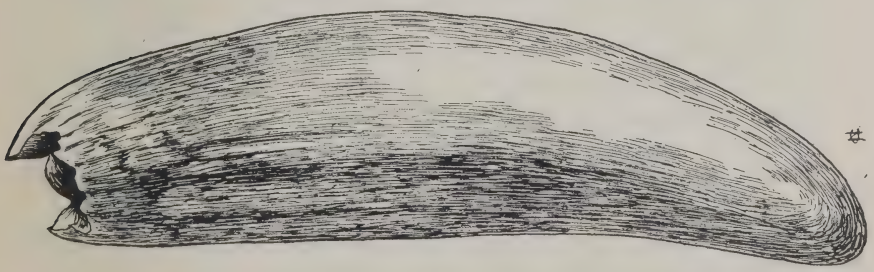


Fig. 208.—Tooth of Sperm Whale (*Physeter macrocephalus*).

the great squids and cuttle-fishes which abound there. In the upper jaw of the sperm whale are numerous rudimentary functionless teeth, deeply embedded in the gum, but the lower jaw contains from twenty to twenty-five stout conical teeth, pointed and recurved, which are attached in a gutter of bone

by a dense fibrous gum ; they are well adapted for tearing off the tentacles of the cuttle-fish.

Enamel is absent from the teeth of the sperm whale, but it was present in the extinct Balænodon. The teeth are formed of dentine, covered with cementum, the axial portion from calcification of the pulp becoming osteo-dentine ; numerous pulp stones of the same tissue are visible at the base of the teeth, and the dentine abounds in interglobular spaces in successive rows, a characteristic of the teeth of Cetaceans.

The *Bottle-nosed Whale* (*Hyperoodon bidens*) also feeds on cuttle-fish. The dentition is reduced to two and sometimes four strong conical teeth, with enamel tips in the front teeth of the lower jaw, and a few small functionless teeth concealed in the gum of both jaws.

Mesoplodon bidens is a whale in which only two teeth are present, situated near the front of the lower jaw ; they are most curious, being thin and strap shaped, attaining a length of 10 inches. They first grow outwards and upwards, and then abruptly curve inwards, over the upper jaw, which they confine, thus limiting the opening of the mouth.

The point of the tooth consists of hard dentine, covered with enamel, the lower part from the bend downwards of vaso-dentine, covered with cementum.

Narwhal (*Monodon monoceros*) is a whale which frequents the Polar Seas. The dentition is represented in the male by one large incisor tusk, which grows horizontally from a large persistent pulp and attains a length of 10 to 12 feet, being embedded in its socket to the depth of a foot. The tusk is spirally twisted throughout its course, with grooves and ridges, winding from right to left, which render it a powerful and elastic weapon of offence. It is sharply pointed, and being present only in the male may be regarded as a sexual weapon, though little is known of its habits. Occasionally two tusks are developed, and in both cases the spiral twisting is from right to left. The tusk consists of osteo-dentine, and is covered by cementum in place of enamel. In the female two incisor germs are retained in their sockets, they become calcified, but never erupt and no other teeth are present, though two rudimentary incisors exist in the fœtus.

Mystacoceti.—The *Whalebone Whale* (*Balæna mysticetus*) is edentulous, the place of teeth is supplied by singular horny

baleen plates, which are attached to the palate and fringe the edges of the upper jaw in numerous rows. Some are from 10 to 12 feet long and each plate is formed of two dense brittle laminæ, enclosing between them a tissue analagous to coarse hairs.

Fig. 209.—Baleen plates of Whale.

In course of time the laminæ break off, leaving a coarse hair-like fringe at the edges of the whalebone plates. They are highly elastic and strong, and fold back when the mouth is closed, but on opening spring forward and act as an efficient sieve or strainer, entangling with the frayed fibres the myriads of small crustaceans and pteropods on which it feeds. So that each mouthful of strained seawater furnishes abundance of highly nutritious food, which is swept off the edges of the whalebone by the large tongue, an adaptation much more efficient than that of the dolphin, which seizes a herring at a time. Each plate is developed by the cornification of the oral epithelium and is nourished by a highly vascular persistent pulp which sends off fine vascular processes far into its substance, so that each hair-like process has a vascular filament at the base. The whalebone whales have pursued an entirely opposite evolutionary course to the sperm whale by suppressing their teeth and substituting in their place an elaborate horny strainer, developed from the cornification of the oral epithelium ; this supplies the animal with a limitless supply of easily digested food, thus enabling it to attain the same gigantic size as the toothed whales. In

the fœtus of the Rorqual (*Balænoptera rostrata*) numerous germs occupy the gutter of the developing jaw, which are never calcified and soon lost, but they indicate a former heterodont dentition by their ancestors in the remote past, being single in front, bifid in the middle and trifid at the back of the mouth.

CHAPTER XVII

UNGULATA

Order—UNGULATA

Sub-order—ARTIODACTYLA, or Even-toed Ungulates.

Group 1. **Suina.**
Families—A. Suidæ (pigs)
B. Hippopotamidæ (hippopotamus)
C. Dicotylidæ (peccaries)
} Teeth bunodont. Non-ruminants.

Group 2. **Tylopoda.**
Family—Camelidæ (camels, llamas)

Group 3. **Tragulina.**
Family—Tragulinidæ (chevrotains)

Group 4. **Pecora.**
Families—A. Cervidæ (deer)
B. Giraffidæ (giraffes)
C. Bovidæ (antelopes, sheep, cattle)
} Teeth selenodont. Ruminants.

Sub-order—PERISSODACTYLA, or Odd-toed Ungulates.
Families—A. Tapiridæ (tapirs).
B. Rhinocerotidæ (rhinoceroses).
C. Equidæ (horses, asses, zebras).

Sub-order—HYRACOIDEA.
Family—Hyrax (conies).

Sub-order—PROBOSCIDEA.
Family—Elephas (elephants).

The first two sub-orders are often classed as Ungulata vera or true Ungulates, and the last two as sub-Ungulata as they do not have true hooves.

Characteristics of the Dentition of Ungulates

1. *Situation.*—In the Suidæ the teeth are in series except in the boar, where the canine tusks project outwards and upwards, outside the mouth ; this is emphasized in the wart hog and still more evident in Babirusa alfurus, where they appear like horns. In the hornless musk deer and others the canines hang down from the upper jaw.

2. *Number.*—In the pig the full mammalian dentition is present, but the immense development of the canines in the wart hog has brought about a great reduction in the cheek teeth, so that in the adult only the third molar remains.

Reduction in the number of teeth is also seen among ruminants, e.g. the sheep has lost all its upper incisors and canines.

3. *Form.*—The pigs have molars with bunodont crowns, the surface having nipple-like cusps. The teeth are also brachyodont, except in the wart hogs, where the third molar is hypsodont.

In the ruminants the molars are bicrescentic or selenodont and vary from a brachyodont pattern in deer to a hypsodont form in oxen.

4. *Structure.*—Enamel is present in all teeth with the exception of the tusks of Babirusa ; it is absent on the posterior surface of the tusks of the boar and wart hog, but the canines of the peccary are entirely covered. It permeates throughout the entire crowns of ruminants and the horse, maintaining a rough grinding surface. Thick deposits of cementum cover the molars, when first erupted, but become worn down in the adult animal.

5. *Attachment.*—In the pig long roots secure the molars in their sockets and the hypsodont grinders of the sheep are deeply socketed. The canines of the hippopotamus, and the cylindrical incisors, are fixed in long sockets, growing from persistent pulps.

6. *Succession.*—Throughout the order a functional milk set is developed and retained for a considerable time.

7. *Jaws.*—In Herbivora the glenoid cavity is shallow, the ascending ramus long, the condyle a flat plane, allowing a side to side movement of the jaw when chewing the cud, for which the pterygoid muscles are well developed.

8. *Functions.*—Omnivorous in the suidæ ; all the others are herbivorous.

Sub-Order Artiodactyla, or Even-toed Ungulates

Group I. Suina

Families—A. *Suidæ* (pigs).

B. *Hippopotamidæ* (hippopotamus).

Suidæ.

Pig (*Sus*).—The dentition of the pig is interesting, because it represents the full mammalian formula of 44 teeth, i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3} = 44$, though some authorities regard the 1st premolar as a retained milk molar. The pigs are omniverous feeders, leaves, fruits, acorns, nuts, and roots constituting their natural diet.

The upper incisors grow in a vertical direction, the central pair being wide apart at the base converging at the apex; they impinge on the horizontal lower incisors, which are elongated, and strengthened by a longitudinal ridge of enamel on the inner surface of each tooth. A short space intervenes between the incisors and canines. In the boar the canines are enlarged into powerful tusks, triangular in section; they grow in a circular fashion from persistent pulps, with widely open roots, and are embedded in deep sockets. The upper

Fig. 210.—Dentition of Pig (*Sus scrofa*).

tusks in erupting curve upwards, outwards and then inwards, presenting the inner face to view, upon which the lower tusks (which are the true weapons of offence) impinge and so maintain sharp edges. These sexual weapons are only developed in the male; they are larger in the wild than in the domesticated boar; it is stated that castration affects their growth. They are protected by thick enamel on the front and sides, arranged in the case of the upper tooth in three bands, but the inner surface is bare, hence the rapidity of the erosion when rubbed together and the resulting sharp point and knife-like edge.

In the female the canines are very small.

The cheek teeth increase in size from the first small premolar, with its compressed cone-like crown with two roots, by stages to the molar, with a broad shallow crown (brachyodont), a grinding surface of rounded tubercles (bunodont) and four roots; the molars increase in size, the third being much the largest, with additional cusps. The pig is a typical bunodont and the molars are of a very primitive type. Milk dentition: i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{3}$, total 28.

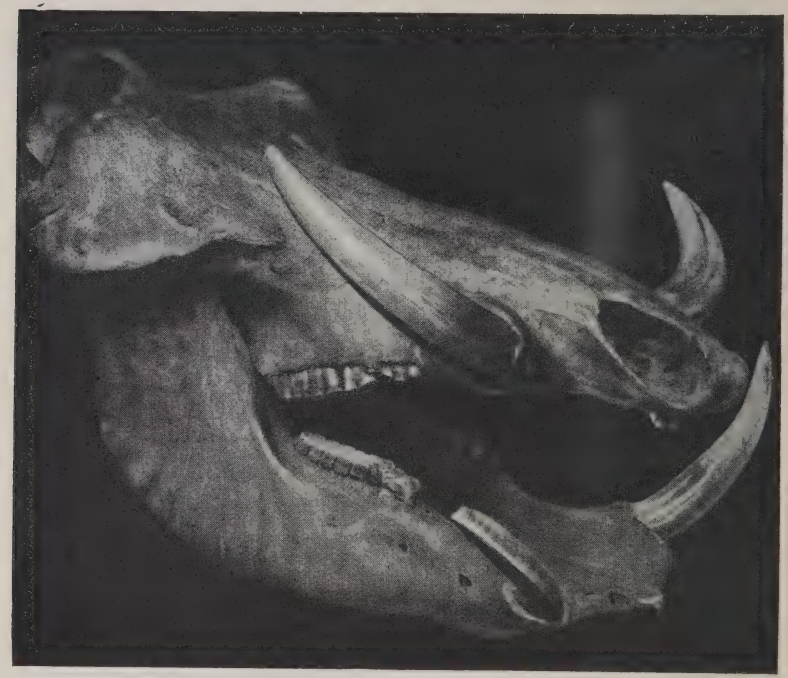


FIG. 211.—African Wart Hog (*Phacochœrus*).

African Wart Hog (*Phacochœrus*) has the canines abnormally developed in both jaws, so much so that room for the cheek teeth is much restricted, and as a consequence they are greatly reduced in size, with the exception of the second and third molars, and are gradually shed from the front, until in aged specimens only the third large molar remains.

This reduction is accompanied by an entire alteration in the form and structure of the last molar tooth, which has varied

from the four-cusped brachyodont type to an enlarged hypsodont tooth of complex character, formed by the union of numer-

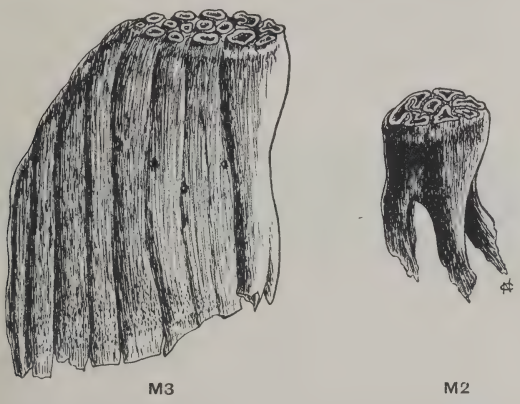


Fig. 212.—African Wart Hog (*Phacochœrus*), Second and Third Upper Molars.

ous cylindrical denticles fused together by thick cementum, resembling the molar of the elephant; it is as large as all the other premolars and molars together. When the occlusal sur-

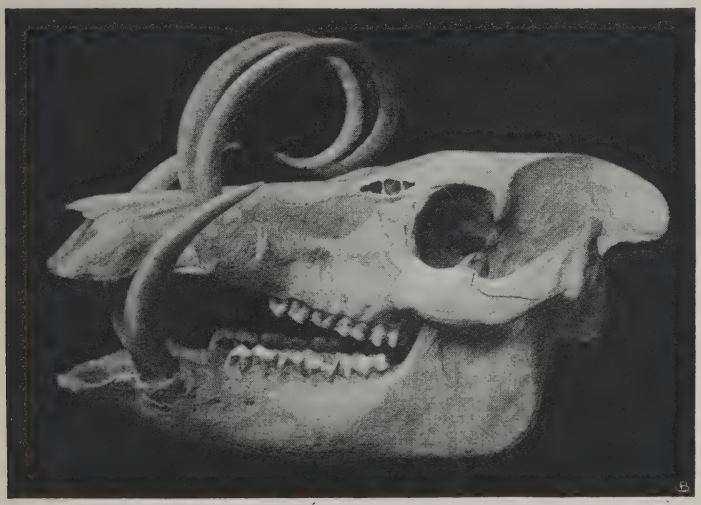


Fig. 213.—Babirusa (*Babirusa alfurus*).

face of the crown is worn the islands of dentine, surrounded by enamel, are exposed, and a rough grinding surface is brought into action by the unequal wear of the tissues; the tooth is of

semi-persistent growth. In the wart hog the canines are large in both sexes. (Fig. 212.)

Babirusa (*Babirusa alfurus*), a strange pig inhabiting the Malay Archipelago, is an apparent example of an aberrant evolutionary form from the excessive growth of the canines, which measure from 8 to 10 inches in length and grow from

FIG. 214.—Hippopotamus (*Hippopotamus amphibius*).

persistent pulps. The upper teeth pierce the lip and curve backwards with the points directed towards the eyes. The lower tusks, failing to antagonize with the upper, continue to grow upwards in a curve, the two pairs appearing as grotesque horns in front of the head of the animal; they are destitute of enamel and apparently functionless, though originally they must have been evolved as sexual weapons, being found only in the male; in the female they are quite small.

The premolars and molars are of the ordinary bunodont character, usually p. $\frac{2}{2}$, m. $\frac{3}{3}$.

Hippopotamidæ.

Hippopotamus (*Hippopotamus amphibius*) is amphibious in its habits; it frequents the lakes and rivers of Central Africa, where it feeds on the lush, aquatic vegetation. The dentition is pig-like but presents some interesting departures; the formula is i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3} = 40$.

The incisors are reduced by one pair and the two remaining pairs are cylindrical tusks, growing from persistent pulps; horizontally in the lower jaw, where they are tipped with enamel, and vertically in the upper, where longitudinal bands of enamel strengthen the teeth; the lower teeth are separated by wide interspaces.

The canines are large, with the shape and arrangement of

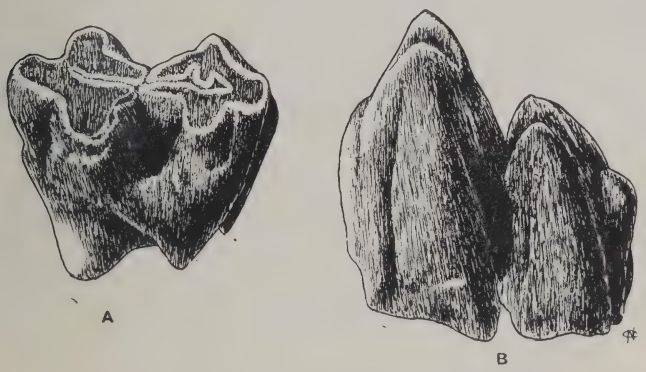


Fig. 215.—Molars of Hippopotamus.
A, worn; B, normal.

the tissues, as in the pig; they are further strengthened externally by numerous thick longitudinal ribs of enamel.

The brachyodont molars have large conical (bunodont) cusps on the crowns, which are at first separated by deep grooves, but the rapid wear produces in time a double trefoil pattern.

Dicotylidæ.

Peccary (*Dicotyles*), a primitive pig-like animal of South America, differs from pigs in that the upper canines are vertical in growth and entirely covered with enamel; the cheek teeth are bunodont and brachyodont.

Group II. Tylopoda

Family—*Camelidæ* (camels, llamas).

The **Camelidæ** includes the camel and dromedary of the old world, and the llama and alpaca of South America.

The *Camel* (*Camelus*) has a dentition of i. $\frac{1}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{2}$, m. $\frac{3}{3}$, total 34. In the upper jaw the outer pair of caniniform incisors are present, and in very young specimens the other two pairs have been observed in an immature condition, but they are lost early, suggesting the path pursued in the evolution of the ruminant dentition. Behind the intermaxillary suture the recurved canines are in position. The lower canine is separated from the incisors and a wide diastema divides the

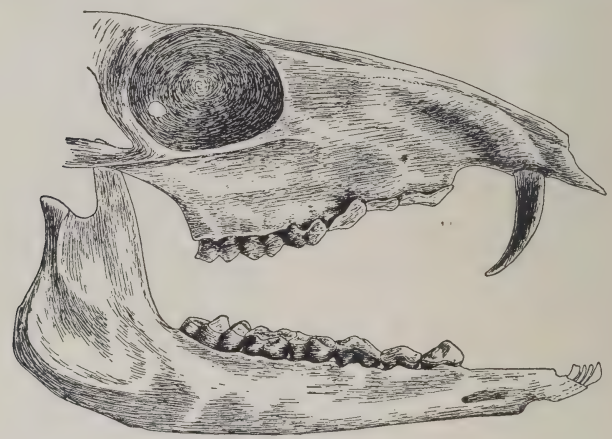


Fig. 216.—Chevrotain (*Tragulus*).

canines from the premolars; the molars are bicrescentic in pattern. In the *guanaco* and *llama* another upper premolar is missing, reducing the cheek teeth to p. $\frac{2}{2}$, m. $\frac{3}{3}$.

It is considered probable that America was the original home of the Camel group as numerous fossil forms have been discovered in the Miocene and Pliocene of that region, linking the camels with more generalized Artiodactyle forms, which are wanting in the old world. The llamas and guanacos of the Andes have lingered on in the ancestral home, while the camels have migrated into Asia, probably across a neck of land connecting Asia and America, now occupied by Behring's Straits.

Group III. Tragulina

Family—*Tragulinidæ* (Chevrotains).

The **Tragulinidæ** family is another link in the selenodont division, for the ruminant characteristics are maintained, such as absence of teeth in the premaxilla, and the selenodont pattern of the molars. But in the *Chevrotain* (*Tragulus*) a small ungulate inhabiting the Malay Peninsula, large upper canines, with persistent pulps, are developed in the male, whose dentition is i. $\frac{0}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3} = 34$; in the female they are very small and functionless.

Fig. 217.—Muntjac (*Cervulus muntjac*).

Group IV. Pecora

Families—A. *Cervidæ* (deer).
B. *Giraffidæ* (giraffes).
C. *Bovidæ* (antelopes, sheep, cattle).

Cervidæ.—The *Musk Deer* (*Moschus moschiferus*) is another example of the retention of the canines, which appear as long, slender, upper tusks, projecting vertically and hanging over the lower jaw. They are evidently intended as sexual weapons as they are small in the female. Being hornless the musk deer and chevrotain would be unprotected but for the presence of the powerful canine tusks. The Chinese *Hornless Water Deer* (*Hydropotes inermis*) is another instance of the upper canines being retained and abnormally developed into powerful

weapons ; they are deeply implanted and project in closure below the lower jaw.

In other deer the same fact may be noticed, but the canines are rudimentary and often wanting in adult skulls.

The *Muntjac* (*Cervulus muntjac*), a small deer inhabiting the Malay States, is an example of large canines being present together with antlers, which is most unusual, and in this instance the antlers, though small, spring from strong bony cores ; the canines are long, powerful, pointed teeth, projecting

Fig. 218.—Sheep (*Ovis*).

from the upper jaw, growing downwards and then outwards in a semi-circular fashion ; in the female they are small and rudimentary. The molars in Cervidæ are somewhat brachyodont. (Fig. 217.)

Bovidæ.—This family comprises the antelopes, sheep and oxen ; dentition, i. $\frac{0}{3}$, c. $\frac{0}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3} = 32$. The cheek teeth in erosion show a crescentic pattern, hence the term selenodont.

The *Sheep* (*Ovis*) is a familiar example of a typical ruminant. In the upper jaw all the incisors and canines have disappeared ; this is characteristic of most ruminants. The loss of the incisors was at so remote a period that not even the trace of a germ now remains, or can be observed in fœtal specimens.

In the lower jaw the eight front teeth, procumbent incisors and canines, bite against a dense pad of gum in the upper jaw, the canines resemble the incisors, and are known as canines only from their position as the fourth tooth from the median line. The cheek teeth are separated by a considerable interval from the canines; the premolars, like the molars, are hypsodont, increasing in size towards the back of the mouth with crescentic ridged crowns; the third molar has an additional lobe. In the ruminants the small rounded condyles allow considerable lateral movement in the jaws, which can be seen when a cow is chewing the cud, the side to side motion grooving the surfaces of the crowns definitely. They also have a milk dentition

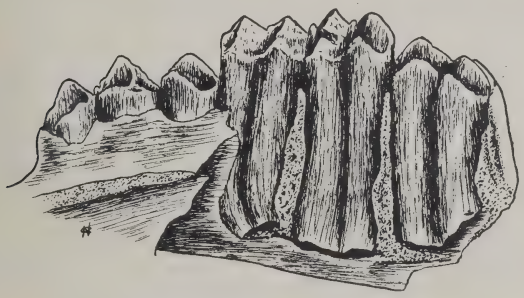


Fig. 219.—Sheep (*Ovis*). Hypsodont molars.

numbering i. $\frac{0}{3}$, c. $\frac{0}{1}$, mm. $\frac{3}{3} = 20$; the first permanent molar is erupted at the sixth month in the sheep and the dentition is completed in the fifth year, in the calf at the fourth year. Ruminants are descended from primitive ancestral types in the Eocene, possessing the full mammalian complement of teeth. Doubtless changes in environment and habits consequent on the appearance of carnivores in the Miocene, which preyed on these unprotected ungulates, had much to do with the alteration in the dentition. Certain teeth were gradually suppressed in the lengthening jaws, others were developed into weapons of offence, as the large canines in the musk deer and muntjac, while some animals were especially provided with antlers or horns. The numerous illustrations still surviving testify to the evolutionary line of the ruminants. Molars vary in shape from the long hypsodont crown of the sheep to the short brachyodont teeth of the deer. (Fig. 219.)

Sub-Order Perissodactyla, or Odd-toed Ungulates

Families—A. *Tapiridæ* (tapirs).

B. *Rhinocerotidæ* (rhinoceros).

C. *Equidæ* (horses, asses, zebras).

The *Tapir* (*Tapirus priscus*), which is now confined to the great river valleys of Central and South America, or the dense forests of Malaya and the East Indies, was once widely distributed, its remains being found in European Miocene deposits and in the Red Crag of Britain. Judging from its teeth it was practically the same as the tapir of the present day. Coming into existence in company with the early ancestors of the horse, it has changed but little through the vast period that has since elapsed; the structure of the brain indicates a primitive type. Its dentition is represented by i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{3}$, m. $\frac{3}{3}$, total 42. It has only lost the first lower premolars. The first and second upper incisors have short wide crowns, but the third are quite unusual, being much larger and caniniform, considerably longer than the true canines. In the lower jaw the incisors diminish in size and the canine is in series with them, biting behind the large upper caniniform incisor. The premolars are separated by a considerable space from the canines, increasing gradually in size; the crowns of the molars are two-ridged, with a valley between (bilophodont), resembling those of the manatee and dinotherium, a primitive form of crown.

Rhinoceros.—The dentition of the rhinoceros varies in the front. Canines are absent in the upper jaw, but sometimes are seen in the lower; the premolars and molars are constant. The formula may be regarded as i. $\frac{2}{2}$, c. $\frac{0}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3}$ = 38. The incisors vary considerably and in the two-horned rhinoceros they are absent. Premolars resemble the molars in size and pattern, the first tooth, as in the horse, being often missing. The pattern of the upper molar crown is less complicated than in horse, the external wall, feeble in tapir, has developed into a prominent ridge, and the transverse ridges (bilophodont), wavy in outline, are obliquely placed, separated internally by a deep valley which is never filled up as in horse; a second valley exists at the back of the posterior ridge. The lower molars are bicrescentic with the concavities facing inwards; the outer wall is continuous.

The rhinoceros was widely distributed in Miocene times, existing both in Europe and America. Numerous remains have been found in the English Pleistocene gravels of the great woolly rhinoceros (*R. tichorhinus*), with immense molar teeth.

In North America there existed in the Miocene numerous allied forms connected with rhinoceros, of which perhaps *Titanotherium* was the most remarkable, a creature resembling the elephant in proportions. (Fig. 197.)

The large brachyodont molars are interesting from an evolutionary point of view, the two outer cusps of the primitive ungulate tooth have become merged into an external wall or sharp ridge of enamel, while the two internal cusps are still

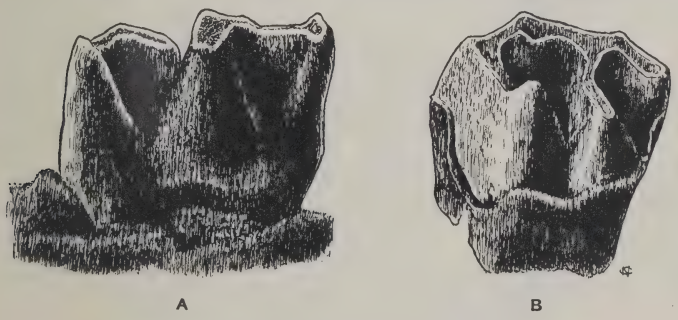


Fig. 220.—Rhinoceros.
A, Lower molar; B, Upper molar.

separate and of bunodont pattern; the basal cingulum is enormously developed, and altogether the crown seems a perfect device for cutting branches with the external sharp ridge and pulping with the rounded tubercles. It is difficult to understand why a creature so well equipped and provided also with a long horn for protection should have disappeared so early, while its cousin the rhinoceros should have remained to the present.

The rhinoceros is now found in Africa, India, and the East Indies.

Horse (*Equus*).—The bodily structure and teeth of the horse have completely changed from the ancestral Eocene forms. The line of its descent can now be traced step by step from a small primitive ungulate, the Eohippus, from the

lower Eocene of N. America, which stood about 11 inches in height, with four toes on each foot, and the rudiments of a fifth, and possessing the typical dentition of forty-four, with shallow brachyodont molars. Various successive fossil forms show the gradual suppression of the toes until in the horse only the central toe remains, enlarged and specialized, with a splint bone on either side, the rudiments of the lateral toes.

The alteration in the foot of the horse has been accompanied by modifications in bodily structure, which are especially apparent in the skull and the teeth ; the latter have completely changed from simple brachyodont crowns to the large and complex hypsodont molars, with long crowns and very short

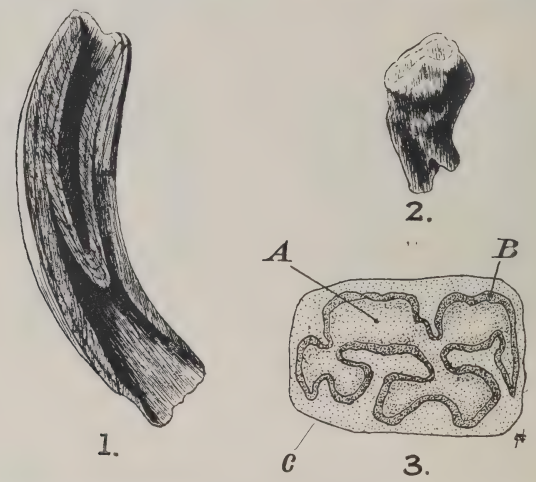


Fig. 221.—Horse.

1, Section of incisor, showing invagination of crown. 2, Functionless first premolar. 3, Horizontal section of crown of molar. *A*, Dentine. *B*, Enamel. *C*, Cementum.

roots. The dentition consists of the typical forty-four teeth, but the first premolar is generally wanting ; it occurs as a small functionless tooth (known as the *wolf tooth*) in front of the premolar series and is early lost ; if it should happen to be retained it often sets up a great deal of irritation and has to be removed. In the successive stages of the descent of the horses the gradual reduction in size is quite apparent, from a functional tooth to a rudimentary and useless one, while the other premolars have increased in size, so much that now they equal the molars in bulk.

The incisors bite edge to edge and the wear is naturally very

considerable ; on the biting surface is to be seen, in a young horse, a deep invagination or hollow in the crown, which is lined with enamel and known to horse dealers as the *mark*.

By the rapid wearing of the tooth the pit or mark gradually disappears, until after about the tenth year it has been entirely eroded and the dark axial portion formed by the calcification of the pulp alone remains, hence the saying, "Do not look a gift horse in the mouth."

The incisors are not persistent, but gradually rise in their sockets as the crowns are worn down.

The mark in the central pair of lower incisors is worn by the end of the sixth year, in the second pair at seven, and in the outer teeth at eight years. In the upper teeth the wear is two years later, and from twelve to twenty-one years the age is told by the longitudinal ridges of enamel on the front of the crowns. The invagination of the incisors is found in no other living animal, but it existed in Hipparion and Macrauchenia.

Fig. 222.—Horse. *A*, Molar, hypsodont; *B*, surface of crown.

The canines are small and wanting in the mare, narrow interspaces separate them from the incisors, and a large diastema divides them from the premolars, caused by the gradual lengthening of the jaws ; the space is used by man for the insertion of the bit, whereby the horse is now controlled.

The premolars and molars, p. $\frac{3}{3}$, m. $\frac{3}{3}$, are large squarish teeth, all touching one another, without interspaces, forming together efficient grinding blocks ; the crowns are long and deeply inserted (hypsodont), with very small roots, and the teeth rise bodily in their sockets as the surfaces are worn, so that in old age they have been so much worn that the crowns are almost destroyed and finally fall out, and the hollowed jaw is filled with a loose cancellous bone.

The grinding surface of the upper molar forms a complex pattern from the irregular winding of the outer wall or ridge

of enamel, which presents a bicrescentic appearance, the concavities looking outward on the external surface and enclosing two islands formed by the transverse ridges, which curve backwards and inwards, the posterior end of the anterior meeting the anterior end of the posterior ridge. Besides this a vertical pillar is added to the posterior end of each ridge, giving to the tooth an appearance of bewildering complexity.

The bicrescentic character of the ridges in the lower molar is well seen, somewhat resembling those of the rhinoceros, but with more wavy and sinuous outlines; to the posterior end of each is also added a vertical pillar.

When first erupted the premolars and molars are covered with a thick deposit of cementum and the extraordinary fusion of the dental tissues makes them admirably adapted for crushing hard and gritty food; the unequal wearing of cementum, enamel and dentine ensures a roughened surface through the enamel ridges remaining less worn, effecting a mill-stone-like aspect, and the more the crown is used, the rougher is the grinding surface.

Milk Teeth.—The horse has well-developed milk teeth, consisting of i. $\frac{3}{3}$, c. $\frac{0}{0}$, mm. $\frac{3}{3}$, which commence to appear just after birth, and are completed by the end of the first year; the molars have the same characteristic pattern as the permanent successors. The first permanent molar appears just after the first year and at the fifth year the dentition is complete.

The horse is unprovided with weapons such as tusks, horns, or antlers for defence, but its superior intelligence and speed enabled it to escape from its enemies and to accommodate itself to the various changes of food and environment throughout the long ages of its existence. It appeared in the older Pliocene of Europe and in the Pleistocene of America.

The gradation in the stages of development in the teeth of Perissodactyles is well seen in the upper molars of tapir, rhinoceros and horse.

1. Tapir, with two simple transverse ridges and a slight development of the external wall.

2. Rhinoceros, in which the transverse ridges have become oblique and the enamel margins wrinkled, especially so at the back of the posterior ridge, where an additional valley has been formed, the external ridge being more sinuous than in the tapir.

3. Horse, in which the transverse ridges bend backwards and lie across the crown, presenting a bicrescentic appearance, with the hollows turned towards the external aspect of the tooth and the enamel margins are very much wrinkled, while the outer wall has become more complex from the additional folding, the external face being bicrescentic, with the hollows of the crescents facing outwards.

Extinct Ungulates

Anoplotherium, from the English and French upper Eocene, was doubtless on the line of the direct descent of the ruminants. Its dentition was i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3}$, total 44, the typical mammalian formula; all the teeth were in series, without a break or diastema, and no tooth was raised above its fellows. The pattern of both upper and lower molars resembles those of rhinoceros. Anoplotherium had the same double crescent in the crown of the lower molars. Numerous extinct forms have been brought to light from the Eocene of Europe and America, suggestive of links between Bunodontia and Selenodontia.

Oreodon had the typical mammalian dentition, but in the lower jaw the tooth doing duty as a canine was the first premolar, which closed behind the upper canine; in this respect it is like the mole. The molars resemble those of ruminants.

Dichobune had the same characteristic, the first lower premolar being caniniform; the molars are bunodont. This animal had the full dental formula.

Cœnotherium likewise had the full complement of teeth, but the molars were distinctly selenodont, and no tooth was raised above its fellows.

Sub-Order Hyracoidea

The *Hyrax family* constitutes the sole representative of this singular order of mammals, which has for so long puzzled zoologists, who first assigned them to the rodents and then to the ungulates.

The hyrax or biblical coney inhabits rocky places in Syria and East and South Africa; in size it is like a rabbit and feeds on leaves and herbage.

The teeth at first sight suggest a rodent, but it is more closely allied to the rhinoceros and is a living example of a very primitive ungulate form.

The dentition is i. $\frac{2}{2}$, c. $\frac{0}{0}$, p. $\frac{4}{4}$, m. $\frac{3}{3} = 36$; the central pair of upper incisors are large and curved, triangular in section, and growing from persistent pulps, as in rodents, with thick enamel covering the antero-external and antero-internal surfaces; the biting edges in wearing develop sharp points

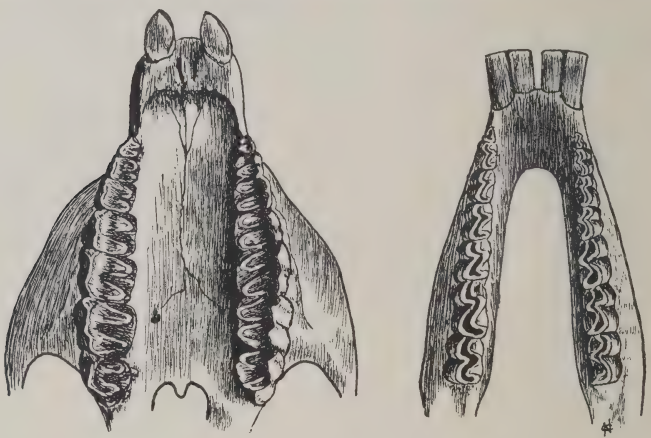


Fig. 223.—Dentition of Hyrax.

rather than chisel edges; the second pair are rudimentary and disappear early.

The lower central incisors are small, with trilobed crowns, and the outer pair, though much larger, do not grow from persistent pulps. A considerable space separates the incisors from the cheek teeth and the canines are absent.

The lower incisors do not antagonize with the upper, but bite behind them on a dense pad of gum; the premolars and molars, which are all present, mimic the grinders of the rhinoceros, with bicrescentic crowns in the lower molars and a rhinoceros-like pattern in the upper teeth.

Hyrax has a milk dentition of m. $\frac{3}{2}$, c. $\frac{1}{1}$, mm. $\frac{4}{4}$, total 30.

Sub-Order Proboscidea

The sub-order *Proboscidea* is at present represented by the Indian and African elephants only, but in the Pliocene and

Pleistocene numerous examples of elephants and mastodons were distributed in the continents of Europe, Asia, Africa and America, and it is safe to say that no group of mammals has been more widely dispersed.

In Britain alone three different elephants succeeded one another, *Elephas meridionalis*, the largest known elephant, which stood 14 or 15 feet in height and lived at the close of the Pliocene, followed by *E. antiquus*, of early Pleistocene date, and *E. primigenius*, the mammoth, a denizen of this country during the arctic conditions of the Glacial period; while Malta and Crete were inhabited by a race of pigmy elephants, not larger than a small pony, 3 to 7 feet in height. The story of the evolution of the elephant is most fascinating and is clearly demonstrated by the recent discoveries of Dr. Andrews in early Tertiary deposits in the Fayum district of northern Egypt, where he unearthed an extraordinary number of fossil forms, which are now on view at South Kensington. These exhibit the various stages in the development of the elephant.

No mammalian form is so remarkable in appearance and unique in structure; its massive proportions and the evolution of its singular trunk are the outcome of slow changes and modifications in the teeth of its ancestors.

Characteristics of the Dentition of Proboscidea

African Elephant (*Elephas Africanus*), dentition i. $\frac{1}{0}$, c. $\frac{0}{0}$, mm. $\frac{3}{3}$, m. $\frac{3}{3}$, total 26.

1. *Situation.*—In the upper jaw are a pair of very large incisor tusks, common to both sexes, growing from persistent pulps; all the other incisors above and below are suppressed together with the canines and premolars.

2. *Number.*—The molars number six on each side, above and below, supposed to be three milk and three permanent; the homology is explained by the dentition of mastodon, where three milk molars are retained. Only one or a portion of two are in place at the same time; the displacement is from behind, the molar gradually moves forward obliquely, and is often worn away in the front before the hinder part has erupted, so different from the ordinary vertical eruption of mammalian teeth.

3. *Form.*—The tusks are cylindrical, with immense pulps at the base, and describe a wide curve in growth, which was greatest in the mammoth.

In the African elephant the tusks are much longer than in the Asiatic variety. The average weight of a tusk is from 20 to 50 lb. each, but specimens from Central Africa have been recorded weighing respectively 225 lb. and 255 lb.

The molars are very large, hypsodont, with poorly-marked roots. They are formed of flattened plates or denticles, united into a grinding block, each plate wearing into a lozenge shape, and each has its own pulp chamber proceeding from a common deep pulp chamber ; when first erupted each denticle is surmounted by numerous rounded cusps. (Fig. 224.)

4. *Structure.*—The tusks are composed of a form of dentine, known as ivory, which is distinguished by its greater amount of organic matter, from 34 to 40 per cent. as compared with 20 per cent. in man, and the numerous secondary curvatures of the tubules of narrow diameter, from which probably the great elasticity of ivory is due. A transverse section shows a structure of decussating lines formed by the intercrossing and curvature of the dentinal tubes, together with numerous concentric rows of interglobular spaces, producing the well-known pattern of ivory.

Injuries from spear thrusts and bullets at the growing end of the root are speedily repaired, the irritation from the presence of a foreign body excites the pulp to enclose it in a covering of secondary dentine ; after which the formation of tubular dentine is continued as before ; and it is only by making a section of such a tooth that the presence of the foreign body is revealed. In old age also the remains of the pulp are converted into secondary dentine.

The tusk, when first erupted, is tipped with enamel, which soon wears away, and the whole tooth is covered with cementum.

In the molars the plates consist of islands of dentine ringed with enamel, the whole united into a grinding mass, whose unworn surface is covered with a thick deposit of cementum. The uneven wear of the tissues exposes the enamel ridges and maintains a rough grinding aspect.

5. *Attachment.*—The tusks are deeply implanted in strong sockets, the molars occupy the hollow jaw, and constantly

move forward, until their grinding surfaces come into action, and when worn are ultimately shed.

6. *Succession.*—The tusks are preceded by small deciduous predecessors, whose ends are tipped with enamel. They erupt between the fifth and seventh month, and are lost before the end of the second year; when fully formed the ends of the roots are closed.

The number of plates in the molars of the African elephant are 3, 6, 7, 7, 8, 10, the first three being considered milk teeth. The tooth plates are diamond shaped.

7. *Jaws.*—In the course of evolution the jaws have been shortened in the elephant and retracted underneath the cranium, as the neck gradually shortened and the trunk lengthened. The lower jaw is a broad gutter, with strong alveolar walls, down which the developing molar travels.

8. *Function.*—The tusks are used in uprooting small trees and shrubs for the animals to browse on the foliage and branches, which would otherwise be beyond its reach; wild elephants are very destructive in young plantations, which they completely wreck by tearing up the young trees. Their trunks are also used in bending down branches to get at the foliage. The tusks are also used as weapons of offence and defence. The molars form efficient grindstones for crushing their food.

Indian Elephant (*Elephas indicus*).—In this animal the tusks are longest in the male, but do not compare in size with those of the African elephant; the female is often tuskless, and in Ceylon, in both male and female, they are often absent.

The plates in the molars are flattened and more numerous, numbering 4, 8, 12, 12, 16, 24, the last being an immense grinder. The usual diet is grass and succulent vegetation.

Ancestors of the Elephants.—*Mœritherium* was a pig-like ancestor of the Proboscidea, recently brought to light in the Fayum, Egypt, by Dr. Andrews, together with various other links in the chain, which help us to trace the descent of the elephant from this lowly origin, and we can follow step by step in its evolutionary story and see the changes wrought by gradual modification of the teeth of the various animals, leading up to the elephant, which have resulted in the complete change of the bodily structure.

Mœritherium was discovered in early Tertiary deposits, a primitive artiodactyle ungulate about the size of a Newfoundland dog, with a short tapir-like snout, pig-like incisors, and bunodont, brachyodont, quadritubercular molars. The dentition was i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3}{3}$, m. $\frac{3}{3}=40$; the second upper pair of incisors were enlarged to form small tusks, which grew from

Fig. 224.—Molar of Indian Elephant (*Elephas indicus*).

persistent pulps, while the first and third pairs were small and rudimentary, demonstrating the homology of the tusks of the elephant, which evolved from the second pair of incisors.

The canines were dwarfed, the cheek teeth all in series, and in use at the same time.

Palæomastodon.—In the next stage, represented by Palæomastodon, a great change is observed; both jaws have lengthened considerably, the incisors are reduced to a pair in each jaw; the lower procumbent teeth are prolonged to keep pace with the constant growth of the upper tusks. Canines are absent, the molars have become lophodont, with three ridges, the cheek teeth are all in series, with milk molars $\frac{3}{3}$.

Tetrabelodon.—In Tetrabelodon the elongation of the jaws and teeth has reached its limit, and has become almost a source of weakness; the antagonism of the incisor tusks very feeble. They have now extended to the length of the skulls so that there is not room for all the cheek teeth to be in together; moreover the molars have greatly enlarged and in the adult only the last two pairs remain. The non-flexible proboscis

has elongated considerably. From this point the lower jaw became gradually retracted, until in the elephant it is shortened and drawn underneath the cranium and the lower tusks are suppressed.

The change affected the upper tusks enormously, which, growing from persistent pulps, and being unable to antagonize with the lower incisors, ultimately developed into the great circular tusks of the mammoth and African elephant.

Side by side with the changes in the teeth was the gradual evolution of the trunk, from the short snout of Mœritherium to the elongated non-flexible trunk of Tetrabelodon. The excessive growth of the tusks and their great and increasing weight imposed an immense strain on the muscles of the neck, and whereas Meritherium was able to feed from the ground the neck of Tetrabelodon, owing to the continuous strain of the heavy tusks, became so shortened that this became impossible, and the snout continued to develop and lengthen into the wonderful flexible trunk with its marvellous sense of touch, an organ which has exercised such an important part in the subsequent life history of the elephant.

Mammoth (*Elephas primigenius*).—The mammoth existed in great numbers in the late Pleistocene period; their remains are found as far south as the Pyrenees, and are also distributed over northern Europe, North America and northern Asia. In the latter place numerous tusks are found embedded in the frozen gravels of the rivers and tundra in the north of Siberia, where a trade in fossil ivory exists.

A few years ago a frozen specimen of the beast was discovered entire with flesh and fur perfectly preserved. The mammoth was contemporaneous with palæolithic man, who has left an engraving of the great elephant scratched on a portion of mammoth tusk in the cave of La Madelaine, France. It shows the long hairs which covered its body as a protection from the intense cold of the glacial period and the huge circular tusks.

Its remains have been found in glacial gravels in Britain and Ireland, and the trawlers in the North Sea frequently dredge up from the Dogger Bank bones and teeth of mammoth. In this elephant the tusks attained their greatest size and curvature, sometimes measuring 9 to 10 feet, and occasionally weighing 200 lb., describing almost a circle.

In the development of the tusks they resembled the African elephant, and in the molars the Indian, but the narrow straight plates in the molars are more numerous.

Mastodon.—The dentition of Mastodon was i. $\frac{1}{1}$, c. $\frac{0}{0}$, mm. $\frac{3}{3}$, m. $\frac{3}{3}$, total 28. The family appeared in the middle Miocene and lasted to the end of the Pliocene, almost to the time of the appearance of man. The mastodons were common both to Europe and America and were of elephantine proportions, with a pair of straight tusks in the upper jaw 7 or 8 feet in length and a pair of smaller tusks in the lower jaw, in some instances provided with longitudinal bands of enamel. The molars are immense with brachyodont crowns, on the grinding surface are several stout, high ridges, with rounded apices,

Fig. 225.—Molar of Mastodon.

separated by deep valleys, such as are seen in the American mastodon (lophodont); in others the crowns are mamillated (bunodont); in both instances rapid wear produces islands of dentine surrounded by ridges of enamel similar to the molars of elephant.

The teeth have long roots and succeed one another vertically, except in the American mastodon, in which no vertical succession has been observed; they increase in size from the front of the series. In some of the mastodons two of the three milk molars were succeeded by two premolars which are small and almost functionless, and in others the premolars are absent, and all the milk molars persist, showing the homology

of the six molars of the elephant, which may now be considered to be milk molars $\frac{3}{3}$, permanent molars $\frac{3}{3}$. The deciduous molars and also the premolars are gradually shed from the front of the series, and the first two molars are lost when the crowns are worn, until in old age only the last molar remains.

Dinotherium.—This was a large animal, probably aquatic in its habits, whose remains have been found in various Miocene and Pliocene deposits on the continent of Europe, in England and in India. It was probably as large as an elephant and is thought to have been of aquatic habits.

The dentition was i. $\frac{0}{1}$, c. $\frac{0}{0}$, p. $\frac{2}{2}$, m. $\frac{3}{3}$, total 22; preceded by milk molars $\frac{3}{3}$. Canines were absent. There were no tusks in the upper jaw, but the front of the lower jaw was bent or deflected downwards at the symphysis, and carried a pair of short, slightly curved incisor tusks, 2 feet long.

The molars are bilophodont like the tapir, with the exception of the first molar, which is three ridged; the succession was vertical.

CHAPTER XVIII

CARNIVORA

Order—**CARNIVORA**

Sub-order—FISSIPEDIA, or TRUE CARNIVORA

Group 1. **Aeluroidea, or Cat-like Carnivora.**
Families—A. FELIDÆ: genus *Felis*, ex. lions, tigers, cats.
B. VIVERRIDÆ: genera *Viverra* (civets), *Genetta* (genets), *Herpestes* (mongooses), and other small genera.
C. HYÆNIDÆ: genera *Hyœna*, *Proteles* (aard-wolf).

Group 2. **Cynoidea, or Dog-like Carnivora.**
Family—CANIDÆ: genera *Canis* (dogs, foxes, wolves, etc.), and other small genera.

Group 3. **Arctoidea, or Bear-like Carnivora.**
Families—A. URSIDÆ: 3 genera.
B. PROCYONIDÆ: racoons, the panda.
C. MUSTELIDÆ: numerous genera: include weasels, pole-cats, skunks, badgers, otters.

Sub-order—PINNIPEDIA, or MARINE CARNIVORA
Families—A. PHOCIDÆ: seals.
B. OTARIIDÆ: fur-seals.
C. TRICHECIDÆ: walrus.

THE animals comprising the order Carnivora are numerous, and of world-wide distribution. The order includes the various beasts of prey, and is divided up into sections and families whose habits and food vary considerably.

While the higher Carnivora are predatory, and true flesh eaters, many others are mixed feeders, and the dentition varies accordingly.

1. *Situation of Teeth.*—The teeth are implanted in the alveolar process. Most of the Carnivora are land animals, but others, such as the seals and walrus, lead an aquatic life.

2. *Number.*—In the dogs and bears the typical mammalian dentition exists but for the absence of the third pair of molars in the upper jaw, while in the cats the cheek teeth are much reduced in number.

3. *Form.*—Incisors usually number six in each jaw, increasing

in size from the first to the third, which is the largest and often caniniform, a characteristic most marked in the upper teeth. The crowns are notched, such as in the dog, and set in a straight line : in the true flesh-eaters they are small in comparison with the big canines. The canines are the characteristic teeth of this order, being strong, recurved, sharp-pointed conical weapons, deeply implanted.

In the blood-sucking animals such as the weasels, the teeth are needle-like in their sharp points.

A knife-like internal edge runs from point to base of the crown in the Felidæ, and is well seen in the tiger. Diastemata exist in the upper jaw between the outer incisors and canines, in which the lower canines close. The premolars and molars vary much with diet ; they are reduced in number, and blade-like in flesh-eaters, but more numerous, broader and tubercular in mixed feeders, such as in molars of the bear and badger.

The premolars are generally compressed pointed cones, increasing gradually in size from the front.

The fourth upper premolar, the largest of the series, is known as the carnassial tooth, blade-like in flesh-eaters, and antagonizes with the first lower molar, which is the opposing carnassial in the lower jaw.

4. *Structure.*—The crowns are formed of ortho-dentine covered with dense enamel, except in the walrus, whose tusks have no enamel, but are covered with cementum.

5. *Attachment.*—The teeth throughout the order are deeply implanted, with long roots. The walrus is the exception, whose canine tusks grow from persistent pulps.

6. *Succession.*—The milk dentition in the Carnivora numbers i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{3}$, total 28, except in Felidæ, where it is i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{2}$, total 26. The deciduous teeth are well developed in land Carnivora, but are rudimentary and functionless in the aquatic Carnivora, such as the seal (*Phoca groenlandica*), the hooded seal (*Cystophora*), and the walrus (*Trichechus*).

7. *Jaws.*—The articulation of the lower jaw is by long transverse condyles working in deep concave glenoid fossæ, in which there is no lateral movement, the length of the canines limiting the opening, and preventing side to side motion of the jaw. In the badger the locking of the condyles is so complete, by reason of the excessive growth of the post-glenoid process, that it is almost impossible to disarticulate them. In the

Felidæ the jaws are short and stout, and the zygomatic arch is abnormally developed, for the attachment of the powerful masseter muscles ; the cranial, occipital, and sagittal crests, and the deep temporal fossæ furnish attachment to the muscles of the neck and jaw, giving to the carnivore its strong grip.

8. *Function.*—The molars are modified to suit the habits of the various families, blade-like in flesh-eaters and tubercular in omnivorous feeders.

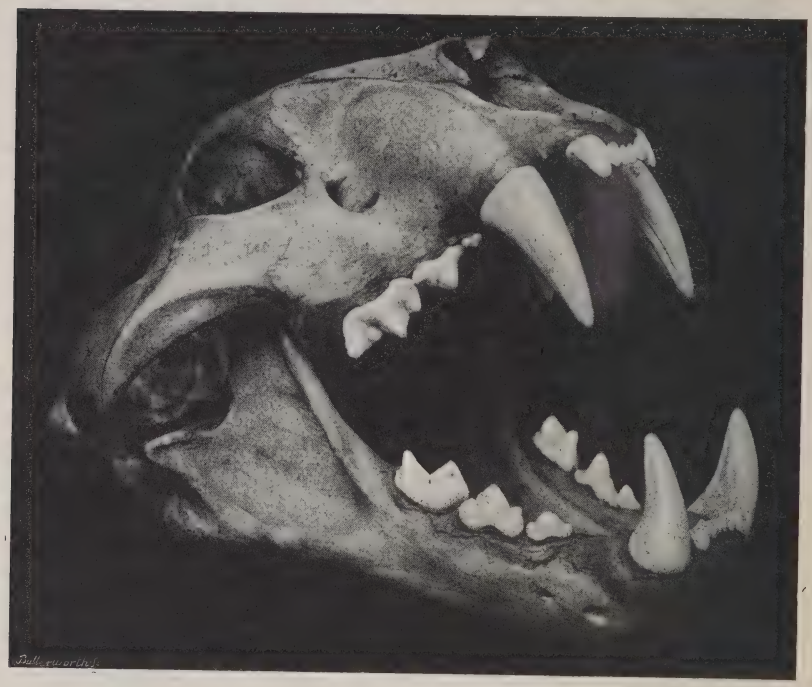


Fig. 226.—Tiger (*Felis tigris*).

Sub-Order : Carnivora vera, or Fissipedia. True Carnivora

Group I. Aeluroidea, or Cat-like Carnivora

Family—A. *Felidæ*, genus Felis ; examples : lions, tigers, cats, leopards, lynxes.

All the Felidæ have the same greatly reduced dentition, numbering i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{2}$, m. $\frac{1}{1}$, total 30. The tiger is a familiar

example. The incisors are very small in comparison with the powerful canines, but stout and thick, arranged in a straight line, and closing edge to edge ; the outermost in the upper jaw is caniniform. A wide diastema separates incisors from canines, in which the lower canines close. The canines are immense, more than half of the crown of each being embedded in a deep strong socket. Along the lingual face of the crown a knife-like ridge runs from the point to the base, which must assist in producing terrible wounds. Behind the upper canine are four cheek teeth ; the first, p. 2, is a small functionless cone ; the second, p. 3, is a conical compressed crown, with a posterior cusp, and the basal cingulum slightly raised on the anterior surface ; the fourth, of very large size, p. 4, is the sectorial or carnassial tooth, being a great blade divided into three external lobes by two deep notches, and on the antero-internal surface a tubercle is developed, which is almost absent in the hunting leopard. The molars are represented by one diminutive functionless tooth, with a tuberculate crown hidden by the carnassial tooth. Behind the lower canine are three teeth, being p. 3 and p. 4, and m. 1. The premolars are compressed cones, with mesial and distal additional cusps, and the flesh-eating molar is a large flattened blade with a V-shaped notch dividing the crown.

The great reduction in the molar series, the shortening of the sturdy thick-set jaws, the enlargement and interlocking of the horizontal condyles, and the deepening of the glenoid fossa, together with the development of the enormous zygomatic arch for the attachment of the masseter muscles, impress one with the perfection of the evolutionary changes ; this is further emphasized by the alteration in the carnassial teeth, which are reduced by flattening the blades to a pair of shears for cutting and slicing flesh, and we feel that in the Felidæ dental evolution in the Carnivores has almost reached its limit.

The Machairodus or *Sabre Toothed Tiger*, an extinct feline form of the early Pleistocene, went a step further, and lost its 1st upper premolar also, reducing its cheek teeth to p. $\frac{2}{2}$, m. $\frac{1}{1}$, and at the same time the canines were abnormally lengthened, so much so as apparently to prevent the animal opening its mouth properly. This may have led to its extermination.

Family—B. *Viverridæ*, genera Viverra (civets), Genetta (genets), Herpestes (mongooses), and other small genera.

The Viverridæ differ from the true cats in having more numerous cheek teeth. The molars are often tuberculated, indicating mixed feeding.

Civet (*Viverra*).—Dentition, i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{2}{2}$, total 40. Only the 3rd molars in both jaws are wanting, the teeth are thicker and stouter, and the anterior internal cusp on the upper carnassial is much larger than in the Felidæ. The molars have broad, tuberculated crowns, showing an omnivorous feeder, and the dentition somewhat resembles that of a dog.

Palm Civet (*Paradoxurus*), with the same dentition, 40. The teeth are still blunter, and have lost much of the carnassial character, the crowns of premolars and molars are tuberculate, having lost the flesh-eating pattern. They are the least carnivorous members of the family.

Mongoose (*Herpestes*), with the same number of cheek teeth, the dentition being 40. In this animal, which feeds principally upon snakes, lizards, small mammals, and young birds, the molars bristle with sharp cusps, which are well adapted for the creature's habits. The mongoose is domesticated in India, freeing the houses and grounds from snakes, rats and mice and other vermin; it is found in Asia and Africa, and one variety in Spain.

Family—C. *Hyænidæ*, genera Hyæna, Proteles (Aard-wolf).

Hyæna, dentition i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{3}$, m. $\frac{1}{1}$, total 34.

Teeth large, stout and strong, deeply implanted in dense, bony sockets. The basal cingulum is abnormally developed to protect the mouth when crushing bones, and the upper carnassial is a very powerful tooth with a large trilobed blade and a pronounced antero-internal cusp. The molar is minute and rudimentary, hidden behind the 4th premolar. Upper and lower premolars are stout compressed cones, the hinder ones with anterior and posterior additional cusps, from the raising of the cingulum; the lower carnassial has a bilobed blade, with an additional small talon.

Aard-wolf (*Proteles*).—The only representative of this genus lives in South Africa. Dentition i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{1}{1}$, total 32. In old specimens several of the teeth are absent. They

are all diminutive cones, unspecialized, and widely separated, showing a degradation from former heterodont teeth to the present rudimentary character by reason of the creature's habit of feeding on carrion.

Group II. Cynoidea, or Dog-like Carnivora

Family—*Canidæ*, genera Canis (dogs, foxes, wolves, jackals, etc.), and other small genera.

The dentition is i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{2}{3}$, total 42. Only the third upper molars are missing. These were present in amphicyon,

Fig. 227.—Fox (*Canis vulpes*).

an ancestral dog-like form from the Eocene, and sometimes appear in domestic dogs. In the examination of a large number of dogs' skulls the author discovered in ten per cent. of the specimens that the third upper molars were present, either erupted or still in their crypts ; so from the evolutionary point of view the dentition of Canis has altered but little since early Tertiary times. (Fig. 227.)

The upper incisors of the dog are small and trilobed, with a transverse groove on the biting edge, the outer pair being the largest.

The canines are stout, conical, recurved, sharp pointed teeth, with an external and internal longitudinal ridge on each crown.

The premolars range from p. 1, a small single-rooted cone, to p. 2 and p. 3, each having compressed pointed crowns with additional cusps on the posterior surface from the raising of the cingulum, and two roots.

The upper carnassial, pm. 4, has a large, stout sectorial crown from which the anterior lobe has almost disappeared, the middle big, conical-pointed lobe (paracone) points backwards, the posterior lobe (metacone) is a laterally compressed blade.

A small anterior tubercle is seen on the lingual surface. Strong roots support the crown, two external and one internal.

The molars have broad tuberculated crowns, signs of a mixed feeder. Molar 1 is about half the length of the carnassial, and considerably wider, the flat surface of the crown is quadri-cuspid. Molar 2 resembles the first, but is more diminutive. The lower carnassial, m. 1, is much the largest tooth in the jaw, blade-like in front with two cusps, the hinder of which is the larger, and a small internal cusp.

The crown is prolonged at the back to form a cusped low talon ; behind are two small tuberculated molars.

The premolars in the dog do not occlude when the jaws are closed, except in the *Cape Hunting Dog* (*Lycaon*), where they interlock, giving the animal tremendous gripping power ; the office of the premolars seems rather to be to pass on the food to the hinder teeth, where it is ground by the powerful sectorial and crushing teeth, immediately underneath the zygomatic arch.

In ordinary dogs the teeth are not crowded ; spaces separate the premolars. This is especially noticeable in the attenuated jaws of the fox, but domestication and selection have in many instances so shortened and malformed the jaws, as in the pug and bull-dog, that there is not room for the teeth to develop normally, and they are crowded and distorted, with the consequence that the third lower molars are missing. In Icticyon, the wild dog of Brazil, this is however a permanent characteristic, while in Otocyon, a fox-like animal of South Africa, the abnormal number of molars is $\frac{4}{4}$, a greater number than in any other living heterodont Eutherian mammal, and in this respect resembling the Marsupials.

The dog being omnivorous, the condyles are more feebly

developed, allowing a certain amount of lateral movement in the jaws.

The Canidæ have a well-marked milk dentition of i. $\frac{3}{3}$, c. $\frac{1}{1}$, mm. $\frac{3}{3}$, total 28. The canines are very slender, curved, and pointed.

Fig. 228.—Bear (*Ursus arctos*).

Group III. Arctoidea or Bear-like Carnivora

Family—A. *Ursidæ :* 3 genera.

The dentition of the bear (*Ursus*) resembles the dog in number, i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{2}{3}$, total 42.

The canines are strong, thick and blunt, the first premolars minute and functionless, often wanting in the adult ; the second and third premolars are often missing.

The fourth upper premolar has lost much of its carnassial character, being smaller than the molar ; the two upper molars have large oblong tuberculated crowns, the second being much the larger. The first lower molar is no longer blade-like, and

the posterior heel has so enlarged that the crown is now broad and tuberculate ; the second and third are similarly shaped, as powerful crushing teeth, m. 3 being the smallest. Such a dentition differs entirely from that of the Canidæ ; the flesh-eating character has disappeared and the broad table-like molars, with strong rounded cusps, are well suited to the mixed feeding habits of the bears, whose diet varies from fish and flesh in the Polar bears, to insects, grubs, fruit, bulbs, roots and honey. Thus they have accommodated themselves to life under intensely varied conditions and diversified food.

The *Malay Bear* (*Ursus malayanus*) is a much modified type, with shortened jaws and large molars, and does much damage in cocoanut plantations.

The bears attained their greatest size in the *Cave Bear* (*Ursus spelæus*), a gigantic creature of Pleistocene age, whose remains have been extensively found in limestone caverns in the British Isles. (See p. 273.)

Family—B. *Procyonidæ :* racoons, pandas.

The only representatives of this family are the *Racoon* (*Procyon*) in North America, and the *Panda* (*Ælurus*) in India.

Procyon has a dentition of i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{2}{2}$, total 40. The premolars are strong serviceable teeth, the hinder ones molariform and cusped, while the molars are broad tuberculated grinding teeth.

It is omnivorous in diet, feeding upon birds, small mammals such as rats and mice, fruit, fish and eggs, for which its strong cusped molars are well adapted.

Family—C. *Mustelidæ*, represented by otter-like (Lutrinæ), badger-like (Melinæ), and weasel-like (Mustelinæ) forms.

The *Otter* (*Lutra*).—Dentition i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{3}$, m. $\frac{1}{2}$, total 36. The upper carnassial has an external tricuspid blade and high and sharp internal ridge, embracing two-thirds of the crown, and a deep concavity separates the ridges. The upper molar is large, table-like, and quadricuspid, its breadth exceeds its length ; the first lower molar has on the external surface an anterior lobe (paraconid), a posterior lobe (protoconid), and an internal cusp (metaconid) ; the hinder part of the crown has a broad cusped talon. The second molar is small, with rounded cusps, implanted at the extremity of the jaw.

Premolars interlock in occlusion, the canines are short, stout, recurved teeth for catching fish, and in this animal the jaws are shortened; the first premolar is lost early.

In the *Sea Otter* (*Latax lutris*), the dentition is i. $\frac{3}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{1}{2}$, total 32. The molars are immense, with broad crowns and large rounded cusps, well adapted for crushing crabs and shell-fish, on which it feeds; it differs from all the other

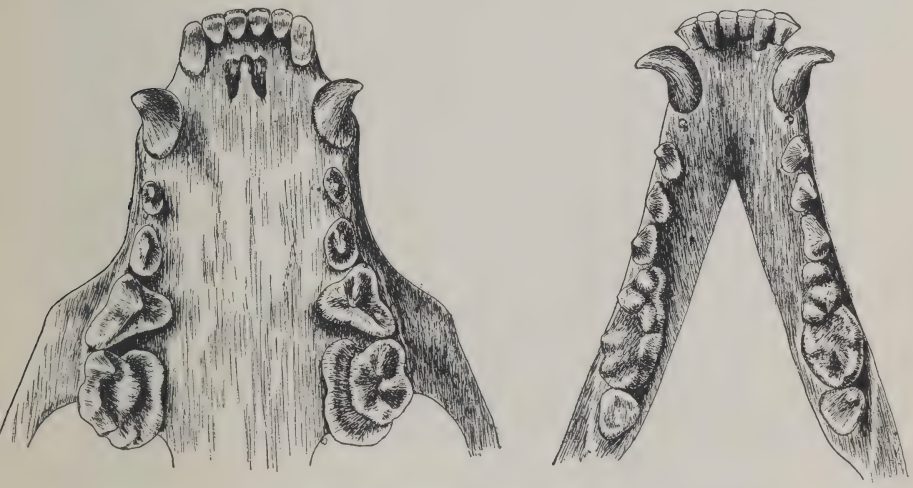


Fig. 229.—Badger (*Meles taxus*).

land Carnivora by the absence of one pair of incisors in the lower jaw, in this respect resembling the seal. In general pattern the teeth resemble the otter's.

In the *Badger* (*Meles taxus*) the upper molar is very much enlarged, presenting a table-like crushing surface, and the first lower molar is also modified, with the addition of a big tuberculated talon, half as large as the crown. The teeth are thus well fitted for the omnivorous diet of the badger, which consists of small animals, reptiles, insects, fruit and roots. The glenoid cavity is also so deepened and enlarged as to interlock the horizontal condyles, which can hardly be separated even in dried specimens. This arrangement gives to the creature immense power in tearing up roots when searching for insects.

In the *Mustelæ*, comprising weasels, stoats, polecats, etc., the dentition is i. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{1}{2}$, total 38. The canines are long and sharp pointed, the upper carnassial has an outer

blade of two lobes, and a small inner cusp, the molar being diminutive, with a tubercular crown. The lower premolars are pointed teeth, the fourth having a distal cusp ; the crown of the carnassial molar has a notched external blade and a feebly developed inner cusp. The dentition agrees with the habits of the family, which are purely carnivorous, their prey consisting of various small animals, as rats, mice, moles, rabbits and birds. They commit great destruction in poultry yards and where game is preserved. (Fig. 230.)

In reviewing the dentition of the terrestrial Carnivora, we are impressed with the modification of the teeth in the different groups and families.

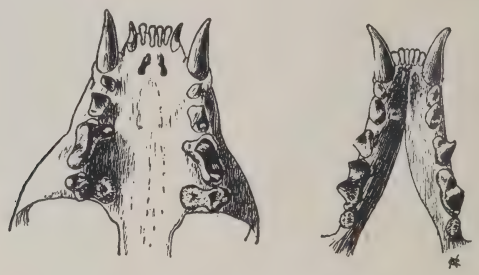


Fig. 230.—Stoat (*Mustela*).

In **Ursidæ,** the premolars are small and feeble ; the molars numerous and well developed.

In **Procyonidæ**, the premolars are better developed ; the molars reduced to $\frac{2}{2}$.

In **Mustelidæ**, the premolars, except for the first one, are better developed still, and the molars still further reduced to $\frac{1}{2}$; they have a superficial resemblance to Felidæ, but even in pure flesh eaters the first molar is a grinding tooth.

Sub-Order Pinnipedia (Marine Carnivora)

The sub-order Pinnipedia embraces the seals and walruses, which spend most of their time in the water, creatures whose remote ancestors led an amphibious life, but afterwards took to a marine existence, for which their bodies and limbs were profoundly modified.

Phocidæ.—The *Seal* (*Phoca*) feeds principally on fishes and crustaceans, and the dentition is i. $\frac{3}{2}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{1}{1}$, total 34. It will be noticed that one pair of incisors is wanting

in the lower jaw, as in the sea otter. The cheek teeth in the *Common Seal* (*Phoca vitulina*) are flattened and blade-like with large central pointed cusps, and additional cusps from the raising of the cingulum, giving a serrated appearance to the crowns. All with the exception of the first tooth are implanted by two roots, a series of minute functionless milk teeth, which includes three deciduous molars, precedes the permanent teeth. The *Fur Seals* (*Otaria*) occasionally have a second upper molar ; the cheek teeth resemble one another and are of a simple pattern. In the *Hooded Seal* (*Cystophora*) they are haplodont.

Common Characteristics of the two Families, Otariidæ and Phocidæ.—The incisors are almost always less than $\frac{3}{3}$, the canines are usually large. The premolars and molars are all alike, and generally much simplified, being triconodont in Otariidæ, and triconodont and even haplodont in Phocidæ. The milk teeth are lost at birth in Phocidæ, and a few weeks after birth in Otariidæ.

Difference between the two Families.—Otariidæ are the least specialized ; they have fur, external ears, and power of land locomotion in the hind limbs. Hence the cheek teeth are not so simple as in Phocidæ, and the milk dentition lasts longer.

Phocidæ are the most specialized, there is no fur or external ear, and they cannot use the hind limbs on the ice ; they have cheek teeth which are sometimes haplodont, and the milk teeth are not functional.

Contrast with Cetacea.—It will be noticed that aquatic habit and the simplicity of a fish diet tend to produce a dentition which is homodont and monophyodont.

In Cetacea (some of which have been derived from a carnivorous ancestry) the process is carried further to completion, and it is probably the milk dentition which survives as the functional set ; in seals it is the permanent one. Phocidæ have taken to the water longer than Otariidæ, and hence have carried the process further.

Trichecidæ.—The *Walrus* (*Trichechus rosmarus*) in the adult state possesses a singular dentition of i. $\frac{1}{0}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{0}{0}$, total 18. Situated inside the intermaxillary bone, a pair of much worn teeth may be noticed, which, from their position within the intermaxillary suture, are undoubtedly incisors ; a pair of huge

upper canine tusks grow downwards from persistent pulps, and outwards in a curved direction, occasionally measuring 30 inches in length, and are used probably for overturning rocks and stones in search of the crustaceans upon which it feeds. They are also of assistance to the animal when climbing on to the ice. The tusks are formed of ortho-dentine uncovered by enamel, the axial portion being of secondary dentine, and a thick deposit of cementum covers the crown ; the dentine of the walrus is

Fig. 231.—Walrus (*Trichechus rosmarus*).

remarkable for the number of concentric lines in a horizontal section. At the back of the upper canine are three much worn cheek teeth, opposed by four similar ones in the lower jaw, the first of which is considered to be a canine. The walrus has a feebly developed milk dentition of rudimentary conical teeth, lost at the time of birth.

Sub-Order Creodonta

In Eocene and Miocene formations, in Europe and America, there have been discovered numerous fossil remains of animals distantly related to the Carnivora, and representing Archaic forms from which probably the Carnivora were descended. They are known as Creodonts. They were animals with small brains, and less specialized teeth than in the modern flesh-eaters, though they suggest hyæna, dog and bear-like stocks.

They differ from the true Carnivora in that the first, second or third upper premolars may transform into carnassials, and they present types of teeth which are transitional between those of the Insectivora and the higher Creodonts, in which the tritubercular character is evident.

Ancestors of the Carnivora.—A generalized carnivorous form is the Proælurus from the upper Eocene and lower Miocene; in the French and American Miocene numerous carnivores appear such as Ælurictis and Archælurus, cat-like animals, and Cynodictis or Viverrine dog; and amphicyon, probably ancestor of the Canidæ, which possessed the third upper molars, wanting in the dog. It is evident that carnivorous forms evolved at a very early date, judging by the researches of Filhol in the upper Eocene of southern France. He discovered a wealth of forms in the phosphorite beds of St. Gérard le Puy, among them forty-two species of beasts of prey.

CHAPTER XIX

RODENTIA, INSECTIVORA, CHIROPTERA

Order Rodentia

Rodents, which number about 900 existing species, have a world-wide distribution. They form a group of small animals of which the largest, *Capybara*, which inhabits the river banks of South America, sometimes attained the length of 4 feet. The greater number are small creatures, represented by hares, rabbits, beavers, guinea-pigs, porcupines, squirrels, lemmings, rats, voles, jerboas, etc. Their habits are herbivorous or graminivorous, feeding on grass, leaves and other vegetation, or nuts, grain, and seeds. They have adapted themselves to various forms of life: some are aquatic, as the beaver, capybara, and water vole, while the squirrel is a tree climber.

The Rodentia are divided unto two sub-orders, *Simplicidentata* and *Duplicidentata*. The former includes the majority of rodents, having only a pair of incisors in each jaw, while Duplicidentata is represented by rabbits, hares and picas, which have two pairs of upper incisors, the second being minute and functionless, concealed behind the great scalpriform teeth and remaining as evidence of the evolution of the rodent dentition from ancestors with the full mammalian dental series. In Australia a rodent-like creature, the *Wombat* (*Phascolomys*), has evolved from a marsupial stock, and in Madagascar the *Aye Aye* (*Cheiromys*) has sprung from a lemurine origin.

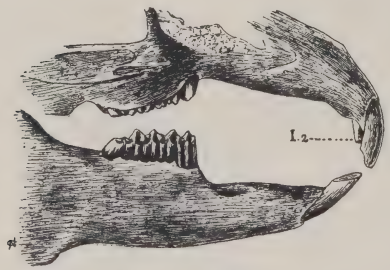


Fig. 232.—Rabbit's dentition, showing I.2.

Characteristics of the Dentition of Rodentia.

1. *Situation.*—A pair of large scalpriform incisor teeth occupy the front of each jaw in the typical rodent, and a long interval on each side separates them from the premolars.

Fig. 233.—Teeth of Squirrel, magnified.

They are large and chisel shaped, semi-circular, and of persistent growth, the large pulp cavities widely open at the base, deeply implanted, and in the lower jaw, as in the porcupine, extending below and behind the molars. They constitute implements of great power for cutting and gnawing. In the rabbit and hare the incisors have a deep longitudinal groove running the length of the tooth. Injury to the jaws from gunshot wounds prevents a rodent getting its teeth together for biting off the herbage, the pain and discomfort cause it to avoid occlusion of the incisors, and the different curves of upper and lower incisors, the upper being a large segment of a small circle, as contrasted with the lower a smaller segment of a larger circle, when once broken by injury prevent contact

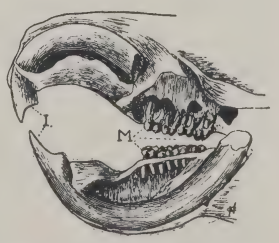


Fig. 234.—Squirrel (*Sciurus*), showing persistent incisors.

from being re-established. The teeth continue to grow in a curved direction, the lower projecting outwards and upwards like the tusks of an elephant, ultimately resulting in the death of the animal from starvation. They are the second pair of incisors, the first and third pair are suppressed.

2. *Number.*—Canines are always missing. The premolars and molars vary in number ; the cheek teeth in the hare number $\frac{6}{5}$, lagomys $\frac{5}{5}$, porcupine $\frac{4}{4}$, rat $\frac{3}{3}$, hydromys $\frac{2}{2}$.

3. *Form.*—Rodents such as the rat and squirrel, whose diet

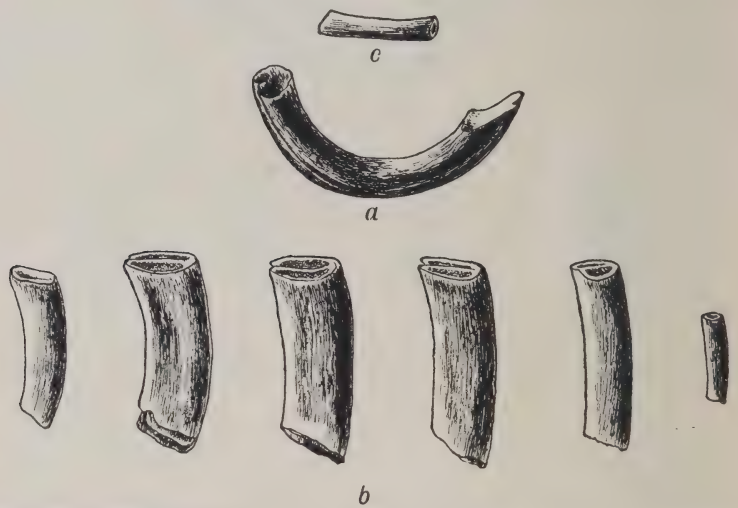


FIG. 235.—Teeth of Rabbit (*Lepus caniculus*). *a*, I.2 ; *b*, molars ; *c*, I.1, magnified.

is omnivorous, or who feed upon hard substances, have short brachyodont crowns, covered with thick enamel ; while the grass and leaf eaters, such as the rabbit and hare, possess curved molars ; premolars and molars are alike in shape and size. They grow from persistent pulps, and are curved to avoid injury in eating to the large vessels in the open ends of the roots.

4. *Structure.*—The incisors are covered with thick enamel on the front and sides, the backs are unprotected, covered only with cementum, which slightly overlaps the enamel edges, hence the backwards and forwards movement of the jaws in eating causes rapid erosion of the lingual surface, resulting in a sharp chisel-shaped biting edge.

In the Australian wombat, a rodent-like marsupial, cementum covers the entire surface of the teeth. In many rodents the enamel is pigmented with an orange-yellow stain, such as is seen in the squirrel, beaver and porcupine. Tubular enamel is found in the guinea-pig, hare and jerboa ; other varieties of complex enamel exist in the teeth of the porcupine and beaver.

Teeth subjected to much hard wear, such as the molars of beaver and porcupine, are of hypsodont growth, the crowns penetrated throughout with curved folds of enamel, which permeate the substance of the crown.

In the Capybara the last large molar is built up of a number of plates of dentine surrounded by enamel, forming islands united together with cementum, resembling the molar of the elephant ; the hard usage maintains a rough grinding surface by the unequal wear of the tissues.

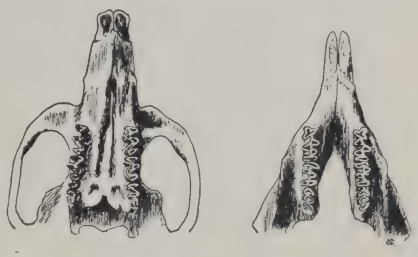


Fig. 236.—Water Vole (*Arvicola amphibius*).

5. *Attachment.*—Besides the methods of attachment already described, squirrels, rats, and mice have the molars implanted with short roots.

6. *Succession.*—The milk dentition is poorly developed.

(*a*) The rat is monophyodont, an exception to the general rule that heterodonts are diphyodonts.

(*b*) Hares have the full set, d.i. $\frac{2}{1}$, d.m. $\frac{3}{2}$. The deciduous molar 1 is absorbed in utero ; the deciduous second incisor and the milk molars are functional, but lost in the third week after birth. They differ from the permanent in being rooted.

(*c*) In the beaver, d.m. $\frac{1}{1}$ lasts until the animal is half grown.

(*d*) The milk incisors, numbering in the squirrel d.i. $\frac{3}{0}$, and in the guinea-pig d.i. $\frac{1}{1}$, are functionless.

7. *Jaws.*—The enormous development of the persistent incisors has caused the jaws to lengthen, and to become narrow and attenuated, and brought about the suppression of all the other anterior teeth, including the canines.

The edge to edge bite of the front chisel-shaped teeth necessitates a backward and forward movement of the lower

jaw. In consequence the condyles have become small and compressed, the glenoid cavity narrowed and elongated to allow this motion, which is characteristic of the gnawing action in eating.

The palate of the guinea-pig (*Cavia*) is so narrow that the premolars of opposite sides almost come into contact in front, blocking the entrance to the mouth.

8. *Function.*—The scalpriform incisors are very powerful and sharp, and excavate holes through timber and even metal ; a rat will gnaw into a gas-pipe, and a squirrel through the hard shell of a nut, while the beaver will gnaw through the trunks of small trees to collect timber to form its dam.

Order Insectivora

The order Insectivora is represented by a class of small animals widely distributed throughout the world, which live on insects, grubs, beetles and worms, and is connected with a very old form of mammalian life, dating back to the Mesozoic period. In Britain the hedgehog, shrew and mole are familiar examples. The *Hedgehog* (*Erinaceus*) has a dentition of i. $\frac{3}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{2}$, m. $\frac{3}{3}$, total 36. The incisors are so arranged as to form an admirable pair of forceps for seizing its prey ; the first upper pair are much larger than the others, rounded and pointed, with a considerable space between them, but they converge slightly at their apices ; the second and third are small pointed teeth. The canine resembles the third incisor, and is but little raised above its fellows, but it is behind the intermaxillary suture, and its root has suggestions of bifurcation ; in some instances it is two-rooted. Of the three premolars the first two are tiny pointed teeth, the last (p.m. 4) is much the largest, having a wide quadricuspid crown, with a big antero-external cusp. The first and second upper molars are quadricuspid with a small central cusp in the middle of the crown of m. 1 when first erupted. They are implanted by four roots, the third molar is small and wedge-shaped, with two roots. In the lower jaw the central incisors are absent, while the second incisors are enlarged to antagonize with the large upper pair, the third incisors being diminutive. The canine is not much raised above the premolars, of which p.m. 4 is considerably the largest. The first and second molars have quadricuspid crowns, and a small additional cusp is observed on the mesial

surface of m. 1 from the raising of the cingulum ; m. 3 is a small conical tooth. The hedgehog has a milk dentition ; a few of the teeth persist after birth.

The Shrew (*Sorex*) is a small mouse-like animal, often seen in the country in early summer, with a long pointed snout ; the dentition is considered to be i. $\frac{3}{2}$, c. $\frac{1}{0}$, p. $\frac{3}{1}$, m. $\frac{3}{3}$, total 32, and is of great interest on account of the modification of the incisors, in which an upper and lower pair have been adapted as pincers for seizing insects. The central, procumbent lower incisors are abnormally elongated, and each is as long as the whole series of cheek teeth, with the upper edge notched, the crown terminating in a sharp-pointed curved tip, fitting—in closure—

Fig. 237.—Dentition of Shrew (*Sorex vulgaris*).
a, Procumbent lower incisor.

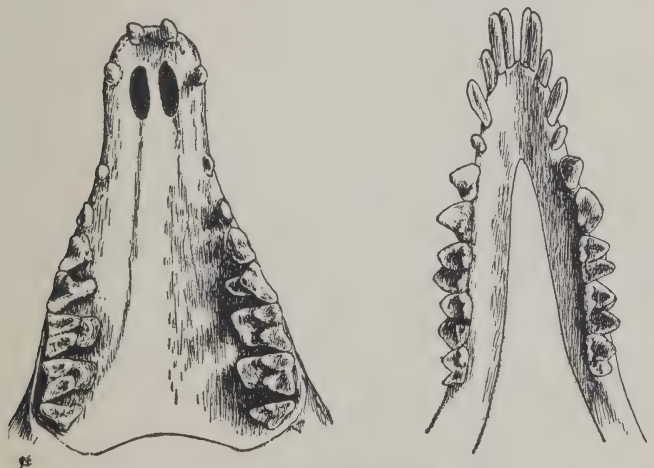


Fig. 238.—Tree Shrew (*Tupaia*).

into a notch in the back of the first upper incisor, which is also a large tooth ; the root end of the lower tooth is prolonged, and actually encases the bone. Fig. (237.)

The dentition of the shrew is puzzling ; some hold the view that there are four upper incisors, because the fourth upper

tooth appears to be in the premaxilla. The molars bristle with sharp cusps and have the W pattern common in the Insectivora ; in embryo it possesses germs of milk teeth, which however never calcify. The enamel of the teeth of the shrew is stained with a chocolate-coloured pigment, and it is also permeated with tubes, a rare occurrence in mammals.

The Tree Shrew (*Tupaia*) of eastern Asia is interesting as linking up the Insectivora and Primates, the six lower procumbent incisors resembling those of the lemurs. Canines in both jaws are small, the upper molars tritubercular. Dentition i. $\frac{2}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 38.

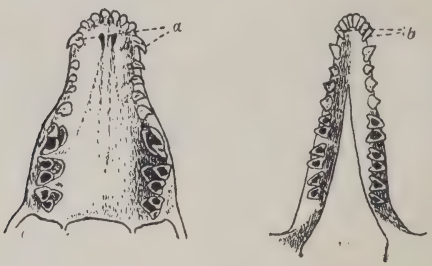


Fig. 239.—Mole (*Talpa europœa*).
a and *b*, canines.

The Mole (*Talpa*) possesses a perfect and beautiful dentition, with the full typical formula of 44 teeth.

In the upper jaw the incisors are small, and the first tooth which calls for remark is the two-rooted canine, which is apparently located in the premaxilla, and has occasioned much controversy as to its real character, but it is now regarded as a canine since in various other Insectivores the canines have been found implanted in front of the intermaxillary suture. The first three premolars are small, conical teeth, the fourth, as in the hedgehog, is molariform. The molars have the W pattern on the crowns of m. 1 and m. 2, which bristle with sharp cusps ; m. 3 is considerably smaller. In the lower jaw the eight anterior teeth have the appearance of incisors, but the outer pair must be regarded as canines, as they close in front of the upper canines, while the tooth which really functions as the canine is the first premolar, a large pointed caniniform tooth, implanted with two roots which closes behind the upper canine. The other premolars and molars resemble the upper,

in the insectivorous character of the crowns. The mole has a set of milk teeth, which are absorbed in embryo. (Fig. 240.)

The *Tenrec* (*Centetes*) of Madagascar, dentition i. $\frac{2}{3}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 38, subsists largely on lizards and snakes, for killing which the long recurved and sharp pointed canines are specially adapted, the points of the lower fitting in pits in front of the upper canines. They are separated by wide spaces from the

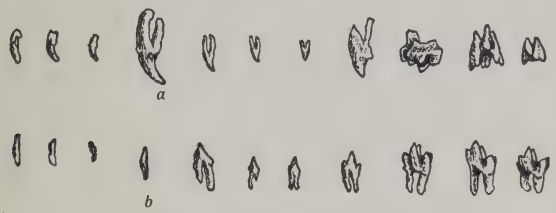


FIG. 240.—Teeth of Mole (*Talpa europæa*).
a, upper canine; *b*, lower canine.

premolars, and give the animal some of the characteristics of a Carnivore. The crowns of the molars are tricuspid, and there is well-marked milk dentition.

Galeopithecus is an aberrant Insectivore, found in the forests of eastern Asia. The dentition is i. $\frac{2}{3}$, c. $\frac{1}{1}$, p. $\frac{2}{2}$, m. $\frac{3}{3}$, total 34. It lives on fruit and leaves, being nocturnal in its habits. The lower incisors are remarkable, the crowns being pectinated, or divided into segments; the upper canine is two-rooted, like that of the mole.

Order Chiroptera

Bats are flying mammals, divided into two sub-orders: insectivorous or insect-eating bats (*Microchiroptera*), a very numerous group, widely distributed throughout the world; and frugivorous, or fruit-eating bats (*Megachiroptera*), inhabiting India, Malaya, and the East Indies.

Microchiroptera, insectivorous bats, resemble in dentition the true Insectivora, especially in regard to the **W** pattern on the crowns of the upper molars, with bristling cusps. The formula of Vespertilio is i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 36, and a wide space separates the upper incisors. Bats have milk teeth, which are shed early, often before birth. The *Vampire* (*Desmodus*), which inhabits Central and South America, has

the teeth curiously modified for its blood-sucking habits ; the dentition is i. $\frac{1}{2}$, c. $\frac{1}{1}$, p. $\frac{2}{3}$, m. $\frac{0}{0}$, total 20. Upper incisors are large, thin, triangular, and sharp pointed, for inflicting the wound, the canines smaller, the premolars diminutive ; the molars are entirely suppressed, not being required.

Megachiroptera.—The *Fruit Bat* or *Flying Fox* (*Pteropus*) is a large fruit-eating bat, found in eastern Asia, with a stretch of wings measuring 5 feet ; dentition i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{2}{3}$, total 34. Incisors are small, but the canines are large. The cheek teeth separated by interspaces, the crowns smooth with a deep longitudinal furrow extending the length of each tooth, encircled by rounded margins. By reason of its fruit-eating habits, sharp pointed cusps are no longer required. Pteropus has deciduous teeth, also consisting of six slender incisors only.

CHAPTER XX

PRIMATES

Order—**PRIMATES**

Sub-Order Lemuroidea.

Families—1. Lemurs.
2. The Aye Aye.
3. Tarsius.

Sub-Order Anthropoidea.

Families—1. Hapalidæ: marmosets.
2. Cebidæ: American monkeys.
New World or Platyrrhine monkeys.
3. Cercopithecidæ: baboons, etc.
4. Simiidæ: anthropoid apes.
Old World or Catarrhine monkeys.
5. Hominidæ: man.

Sub-Order Lemuroidea

Lemuridæ.—The family Lemuridæ is now principally confined to the island of Madagascar, where the mammals are mostly lemurine, but a few representatives occur in Central and East Africa and others in the East Indies, suggesting a continental land connection in the remote past.

The sub-order Lemuroidea is an extremely old one, originating in the dawn of the age of mammals. Fossil forms from the early Eocene intimate a connection between the Lemuroidea and Insectivora.

The lemurs differ from Anthropoidea in the lack of the bony division between the orbit and temporal fossa.

They lead an arboreal life, rarely descending to the ground, living upon fruit, leaves, insects and eggs, and upon small birds and lizards, and are nocturnal in their habits. The dentition is i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 36.

The upper incisors are very minute and vertical, separated

by a space in the middle, the lower incisors are attenuated and procumbent, resembling the teeth of a comb.

The upper canines are long, compressed, curved and sharp-pointed. The lower lie horizontally by the side of the incisors, which they closely resemble, and the tooth which does duty for the lower canine is the first premolar. Its homology is

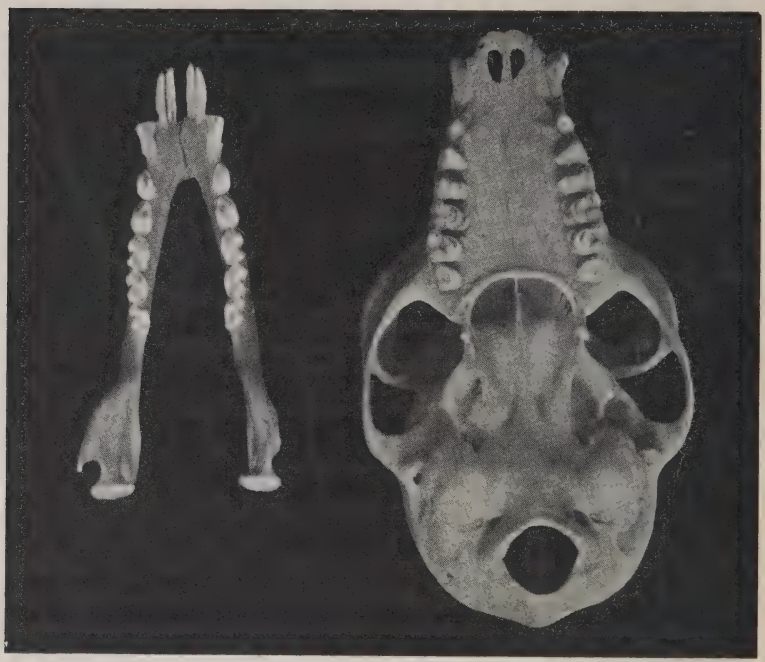


Fig. 241.—Lemur (*Lemur varius*).

evident, as it closes behind the upper canine, and the whole arrangement recalls that of the mole.

The premolars have a pointed cusp externally and an inner tubercle, the molars are quadricuspid, and in some instances tricuspid. The deciduous formula is i. $\frac{2}{2}$, c. $\frac{1}{1}$, mm. $\frac{3}{3}$, total 24. Some of the early Eocene lemurs, such as Adapis, had four premolars, which is not the case with any living primate, and the upper molars were tritubercular.

The **Chiromys**, or Aye Aye, is an aberrant form, living in the forests upon fruit and insects.

Just as in the Marsupialia in Australia a rodent-like animal has been developed, so in the great island of Madagascar a small rodent-like form has been produced in the aye aye. The dentition is i. $\frac{1}{1}$, c. $\frac{0}{0}$, p. $\frac{1}{0}$, m. $\frac{3}{3}$, total 18.

Unlike rodents it has a well-developed milk dentition, which is lost early, and is of lemurine character. In the permanent set a pair of curved chisel-shaped incisors grow from persistent pulps in each jaw. A thin coating of enamel protects the outer surface of the upper teeth, in the lower it is very thick. The molars are small and rooted, the crowns have rounded cusps, for an omnivorous diet.

The **Tarsius** inhabits the forests of the Malay Archipelago ; insectivorous and nocturnal in its habits, it is a rare animal, being seldom seen, as it sleeps during the day. It is about the

Fig. 242.—Tarsius (*Tarsius spectrum*).

size of an English squirrel, with large prominent eyes and ears, and can assume the erect attitude when necessary. The dentition is i. $\frac{2}{1}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 34. The central upper incisors are large and pointed, in this respect resembling the shrew ; the laterals are minute, as are also the lower incisors. The canines are hardly raised above the other teeth, and there is no break in the continuity of the occlusal surface ; the small conical premolars gradually increase in size towards the back of the series. The jaws, pointed in the front, diverge widely in the molar region.

The tricuspid molars have two external and one internal pointed cusps, suggesting an affinity with the Insectivora ; the lower molars are quadricuspid.

Tarsius is regarded as the lowest of the Primates, for ancestral forms, such as Anaptomorphus, which appeared in the Eocene of North America, so closely resemble it that there is but

little difference in the dentition of the two animals, notwithstanding the enormous period of time which separates them. Tarsius links together the Insectivora and Primates.

The differences between Tarsius and other lemurs are principally :

1. Tarsius has only one pair of lower incisors, which are erect, not procumbent.

2. The canines do not interlock ; there are no interspaces, and the lower canines are not procumbent.

3. The orbit is almost shut off from the temporal fossa, such as in monkeys and man.

Sub-Order Anthropoidea

1 and 2. *Situation and Number of Teeth.*—The teeth of Anthropoidea occupy the maxillary, intermaxillary and mandibular bones ; in lemurs and monkeys of the New World they number 36, being i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, but in monkeys of the Old World and in man a pair of premolars in each jaw are suppressed, the teeth numbering i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{2}{2}$, m. $\frac{3}{3}$, total 32. This, together with the loss of a pair of upper and lower incisors, has effected a great reduction from the typical mammalian dental formula.

3. *Form.*—In the monkeys and man the upper incisors are strong squarish teeth, with flat biting edges ; the centrals are much larger than the laterals, and this is especially evident in the baboons. In man the central pair of lower incisors are the smallest ; in the gibbon is the same feature, but the reverse is the case in the baboons, where the lower centrals are much the largest. In the orang-outang and chimpanzee both pairs are equal. The canines vary considerably, and in monkeys of the Old World form powerful sexual weapons in the male baboons and anthropoid apes, where they are enlarged into massive tusks for fighting purposes. In the females they are but feebly developed, projecting but slightly above the other teeth. The premolars vary considerably. In the marmosets the first pair are caniniform, the first lower pair are enlarged and bent backwards in the baboon, while they are biscuspid in the anthropoid apes and in man.

4. *Structure.*—The teeth are formed of ortho-dentine, with a central pulp chamber, enamel covers the crowns, thickest on

the masticating surface, thinnest at the gum margin, and cementum covers the roots and slightly overlaps the edge of the enamel.

5. *Attachment.*—The teeth are implanted in deep sockets, the incisors and canines by single roots. The premolars of the catarrhine monkeys and anthropoid apes are three-rooted in the upper jaw and two-rooted in the lower, while in man all are single-rooted.

The molars have three roots in the upper jaw and two in the lower, in both monkeys and man; they are widely separated in the apes, and except in the first molars are often more or less united in man.

6. *Succession.*—A well-developed milk dentition precedes the permanent set, and is functional for some long time in the Anthropoidea, numbering i. $\frac{2}{2}$, c. $\frac{1}{1}$, mm. $\frac{2}{2}$, total 20, in the catarrhine monkeys and man.

7. *The jaws* are stout and thick, with squarish rami in the monkeys, but destitute of a chin on the mandible; in man they are more slender, with a well-developed chin.

8. *Function.*—The rounded cusps on the molars of both jaws indicate the Anthropoidea as fruit, grain and nut eaters; the teeth are generally adapted for a mixed diet.

Family—A. **Hapalidæ** (*Marmosets*).
Dentition, i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{2}{2}$, total 32.

The marmosets are the smallest of the monkeys, living in the Brazilian forests, where they spend an arboreal existence feeding on fruit and insects. They are active and beautiful little creatures, about the size of a squirrel, and, like all the South American monkeys, have prehensile tails. The teeth in the lower jaw are in a continuous series as in man.

The incisors in the upper jaw are human-like; in the lower jaw they are long, narrow, and of equal size, biting edge to edge with the upper; the lower canine bites into a space between the upper canine and incisor.

The upper canines are long and sharp-pointed, the lower recurved, with a small inner tubercle. The premolars in both jaws are sharp-pointed externally; the inner tubercle is small in the first bicuspid, and increases in size to the third; the roots are single. The upper molars are tricuspid, and the lower quadricuspid; the third molars are missing.

Family—B. **Cebidæ.**

Dentition, i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{3}{3}$, m. $\frac{3}{3}$, total 36.

The Cebidæ, like the marmosets, are found in tropical South America. They differ from the monkeys of the Old World and from man in being wide-nosed (platyrrhine), in having a third premolar in each jaw, and in having prehensile tails. The *Spider Monkey* (*Ateles*) and the *Capuchin* (*Cebus*) are examples.

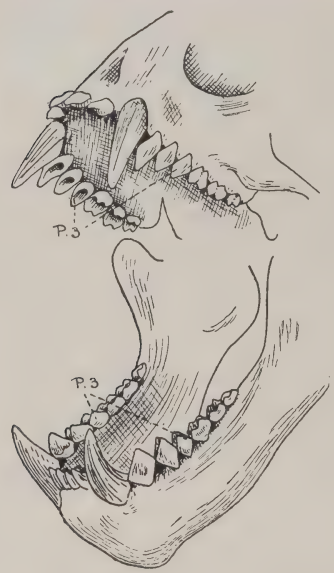


Fig. 243.—Spider Monkey (*Ateles*).

In this family the lower lateral incisors are caniniform, the canines strong and well developed, the upper having a deep anterior groove running the length of the crown. There is a diastema in the upper jaw between the second incisor and the canine, in which the crown of the lower canine closes.

Of the upper premolars the first is the largest, with a small inner tubercle; the second and third are bicuspid and two-rooted. The first lower premolar is large, double the size of the second premolar, with the outer cusp pointed and caniniform, the inner feeble: the second and third crowns are bicuspid, and all have single roots. The upper molars are quadricuspid, with the oblique ridge as in man, implanted by three roots in m. 1 and m. 2, fused in m. 3, which is the smallest tooth. The lower molars are four cusped, with two roots, the third molar being the smallest. In the pattern of the crowns with the oblique ridge on the crown of the upper molars, and the reduction in size of third, the dentition approaches the human more than that of the catarrhine monkeys of the Old World.

Family—C. **Cercopithecidæ.**

Dentition, i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{2}{2}$, m. $\frac{3}{3}$, total 32.

This family includes all the monkeys of the Old World, with the exception of the anthropoid apes (Simiidæ). They are known as narrow-nosed monkeys (Catarrhine) and the tail is not prehensile. The baboons, macaques and langur

monkeys are examples. The dentition is further reduced by the loss of a second pair of premolars in each jaw, which is also a characteristic of the teeth of anthropoid apes and man.

The *Baboon* (*Cynocephalus*) represents the lower members of this family. It has large and powerful jaws, projecting forwards like those of a dog (prognathous). The incisors are large, broad and thick, the lower centrals being larger than the laterals; the opposite is the case in man. They are arranged in a slight curve and bite edge to edge. A wide diastema exists in the

Fig. 244.—Cercopithecus.

upper jaw for the reception in closure of the lower canine. In the male the canines are immense, developed into recurved weapons of offence, triangular in section, the crowns laterally compressed, and while a deep longitudinal groove runs from the base to the point of the crown externally, a knife-like edge traverses the whole length of the lingual surface. The teeth are implanted in deep sockets when the mouth is closed, they project enormously, descending to a depth of two-thirds of the mandible, and rest upon the anterior face of the first lower premolars; indeed, this tooth appears bent backwards by the occlusion of the powerful upper canine. (Fig. 244.)

The lower canines are also very large, curved and sharp-

pointed ; in the female they are small in both jaws and project but little.

The first upper premolar is small with a sharp-pointed outer and feeble inner cusp ; the second has a larger bicuspid crown and both are implanted by three roots. Of the lower premolars the first is a singular-looking tooth, fixed by two roots ; its blade-like crown slopes from the distal angle, and a small pointed tubercle rests on the posterior root. The upper canine, when the teeth are closed, rests upon the sloping crown of this abnormal tooth. The crown of the second lower premolar is compressed and bicuspid ; both teeth are two-rooted.

The quadricuspid upper molars increase in size from the first to the third, the first being much the smallest ; the oblique ridge is absent from the crowns, and all are three-rooted. The lower molars have the same bunodont character in the crowns ; the first two are quadricuspid, but the third becomes quinquecuspid by the addition of a hinder lobe ; all are two-rooted. In consequence of the great size of the canines the intermaxillary suture remains open throughout life.

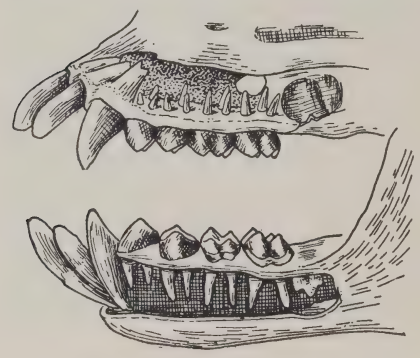


Fig. 245.—Macacus Rhesus.

The dentition of the *Macaque* (*Macacus*) and *Langur* (*Semnopithecus*) *monkeys* is similar, but the first lower premolar is not so bent as in the baboon, and in the *Vervet monkey* the third lower molar is quadricuspid. (Fig. 245.)

The cheek teeth in Cercopithecidæ are arranged in parallel lines, which converge at the back.

Family —D. **Simiidæ. Anthropoid Apes.**

This family is represented by the gibbon and orang-outang of Eastern Asia and the Malay Archipelago, together with the chimpanzee and gorilla of Western Africa. They are known as the man-like apes from the erect position of the body, and their human characteristics.

The Gibbon (Hylobates) leads an arboreal existence, for which its long arms are peculiarly adapted, enabling it to swing

from branch to branch and to travel in the jungle at great speed. Its food consists of fruit, birds, eggs and insects, and when on the ground it can assume the upright position. It is the smallest of the anthropoid apes, of a gentle nature and easily tamed. The dentition in some respects is more human-looking than that of the larger anthropoids, especially in the reduction in size of the third upper molar.

The upper incisors are human-like and small, the laterals being slightly smaller than the centrals; the lower incisors of the central pair are smallest.

Fig. 246.—Cheek teeth of Gibbon.

The upper canines are long and sharp-pointed; the crowns are triangular in section, with an internal longitudinal sharp ridge, and a groove externally running down the length of the crown. The lower pointed canine closes in a diastema between the upper canine and incisor; of the upper premolars the first is the smallest; it is bicuspid, the external cusp being pointed; they have three roots, two external and one internal. The lower premolars differ, the first has a long narrow compressed sharp-pointed crown, slightly raised, implanted by two roots placed anteriorly and posteriorly; the second is smaller, bicuspid and two-rooted. Of the upper molars the second is the largest, the third being much smaller. They are quadricuspid, with an oblique ridge uniting the anterior internal and posterior external cusps; each tooth has three distinct roots, the two outer buccal, the inner palatal. Of the quinquecuspid lower molars the second is the largest, the third smallest; all are two-rooted.

Characteristics of the Dentition of the Gibbon.—The incisors are small and human-like, the canines very long; the crowns of the molars are more rounded than in the catarrhine monkeys, the four tubercles on the unworn upper molars are pointed, and much raised, the oblique ridge is low, and the second molars are the largest.

Orang-outang (Simia).—This is a very large and powerful ape and extremely savage, standing about 4 feet in height. Great supraorbital ridges give the animal a ferocious aspect and a vertical crest crowns the skull.

The upper incisors are very large, strong and thick, the unworn crowns of the laterals being pointed; the lower

central incisors are the largest, the laterals being caniniform.

In the male the upper canines are long, sharp-pointed and powerful, extending in closure below the lower alveolar border of the mandible; the anterior groove is wanting and the internal ridge is less sharp. The lower canines are stout, closing in front of the upper in the wide diastema separating the canine from the outer incisor. In the females the canines are small, not much raised above the level of the others, and no space separates the upper canine from the incisors.

Fig. 247.—Upper cheek teeth of Orang-outang.

Of the premolars the first upper is caniniform, with a small inner cusp; the second is bicuspid, with broader crown; both are three-rooted. The first lower premolar is pointed with a small inner tubercle, the second being quadricuspid; both are two-rooted.

All three of the upper molars are of almost similar size, the crowns are large, broad and thick, covered with wrinkled enamel, a characteristic of the molars of the orang-outang; the oblique ridge is very pronounced, and the three roots are long and widely divergent. The crowns of the lower molars are of equal size, quinquecuspid, three cusps external and two internal. The cheek teeth are arranged in parallel lines converging at the back.

The jaws are prognathous, stout, and powerful; the mandible is chinless.

Characteristics of the Dentition of the Orang-outang.—Central incisors human-like, but large and very thick; lower centrals largest, laterals pointed. Canines immense and stout in the male; roots of premolars and molars long and divergent; enamel wrinkled.

Fig. 248.—Upper cheek teeth of Gorilla.

Gorilla (Gorilla Savagei).—The gorilla is the largest of the anthropoid apes, measuring $5\frac{1}{2}$ feet in height; it inhabits the forests of Western Equatorial Africa. The large round orbits

and great supraorbital ridges in the skull render its appearance repellent.

The zygomatic arch is stout; the ascending rami of the mandible are broad, with shallow sigmoid notches. The incisors are thick and strong, the lower centrals being the smallest, a human characteristic.

The canines in the male are immense and give to the jaws a square appearance; the upper grow downwards and outwards in closure beyond the margin of the lower jaw; wide diastemata separate the upper canines and incisors. In the female the canines are much smaller, erupting after the second molars. The upper premolars are very large and bicuspid, each with three divergent roots. In the lower, the first tooth is bicuspid, a transverse ridge uniting the low internal cusp to the external, while the second is quadricuspid; both are two-rooted. The second is the largest molar in both jaws. The characteristic molar pattern of the crowns of Anthropoid apes and man is well seen; the lower molars are all quinquecuspid, those of the orang-outang having three external and two internal cusps. In the orang-outang the roots are all separate and divergent, three in the upper molars and two in the lower, and are longer in proportion than the roots of these teeth in man.

Characteristics of the Dentition of the Gorilla.—Great size of skull and mandible. Teeth large; sexual difference in big canines of male. Lower central incisors smallest. Second molar largest. Cheek teeth in parallel rows.

Chimpanzee (*Anthropopithecus*).—The chimpanzee is the most man-like of the anthropoid apes, with the nearest approach to the human dentition. The character of the skull is less brutal, the supraorbital ridges are less pronounced, and the jaws are feebler than in the gorilla. The teeth are less massive and arranged in a wider curve, lacking the marked parallel lines of the other anthropoids, but the convergence of the third molars is still apparent.

Fig. 249.—Upper cheek teeth of Chimpanzee.

The incisors resemble those of man but are stout and thick;

the distal angles of the laterals are rounded, and the bite is edge to edge.

The canines, which are largest in the male, are less massive than in the gorilla and orang ; the diastemata in the upper jaw are narrower ; only the points of the lower canines bite into them.

The premolars are human-like in the upper jaw, the crowns bicuspid, with the outer cusps largest. The first lower premolar has the crown slightly bent, reminding one of the same tooth in the catarrhine monkeys.

The molars in both jaws are almost equal in size, if anything the third is slightly the smallest, and they have the characteristic anthropoid pattern on the crowns.

Characteristics of the Dentition of the Chimpanzee.—The incisors are human-like. Canines shorter, diastemata narrower, premolars and molars smaller than in the orang-outang and almost equal in size, arranged in wider curve ; greatest width of palate between upper canines.

The intermaxillary suture remains open through life in the orang-outang and gorilla, but closes after the completion of the dentition in the chimpanzee.

In the anthropoid apes the tongue is attached to the chinless mandible in a deep pit at the symphysis, with a shelf of bone beneath it, instead of to tubercles, as in man.

Milk Dentition.—All the anthropoids have a well-marked milk dentition, which is more human-like than the permanent teeth. The canines project but little, and the diastemata in the upper jaw are very narrow.

Characteristics of the Jaws and Teeth of Anthropoid Apes

1. Massive character of the jaws and teeth, prognathous.
2. Facial angle small.
3. Intermaxillary suture remains open throughout life except in chimpanzee, where it closes after the completion of the milk dentition.
4. Absence of chin.
5. Tongue attached in front to deep pit at symphysis.
6. Squareness of jaws in front from great size of canines.
7. Canines, sexual weapons, erupt in males, after cutting third molars ; except chimpanzee, where they erupt after the second molar.

8. Wide diastemata in upper jaw between canines and incisors to receive lower canines in closure.

9. Incisors thick, bite edge to edge, upper premolars three-rooted, lower two-rooted. Upper molars large, human pattern of crown increasing in size towards the back of the mouth, three long distinct roots. Lower molars quinquecuspid, cusps always distinct with no fusion as in man, two distinct long roots.

10. Lateral movement of mandible restricted by reason of the great length of the canines, ascending rami wide and sturdy, shallow sigmoid notch.

Fig. 250.—Parapithecus.

Extinct Primates

At the commencement of the Eocene, in the dawn of the age of mammals, there is evidence that primitive Primates were even then in existence. Anaptomorphus, of the American lower Eocene, and Microchœrus, from British rocks of the same age, closely resemble Tarsius of the present day. Professor Fairfield Osborn writes, "there can be no question of the near relationship of the two."

Early Lemuroid forms existed in America and Europe possessing premolars $\frac{4}{4}$, such as Hyopsodus, of the American Eocene, and Protoadapis, of the Rheims lower Eocene beds.

Platyrrhine monkeys appeared in Patagonia, South America, in the Miocene, where they have remained practically unchanged to the present day.

In the Oligocene there existed Parapithecus and Propliopithecus, in lower Egypt, two very interesting mandibles of which have been recently brought to light by Professor

Schlosser, and have excited much attention ; they are regarded as small primitive anthropoid apes, probably as large as a squirrel, with a dentition of i. $\frac{2}{2}$, c. $\frac{1}{1}$, p. $\frac{2}{2}$, m. $\frac{3}{3}$, total 32. The teeth are in series and there are no interspaces, the canines not being raised. The molars are quadricuspid, the second being largest, and the teeth are arranged in a curve, diverging at the back, the human pattern being approached at this remote period. (Fig. 250.)

During the Miocene Europe became the home of numerous monkeys and anthropoid apes.

Hylobates antiquus, from the French Miocene, was an ancient form of gibbon, with small canines and no diastemata, while Dryopithecus, another French Miocene anthropoid ape, was probably as large as the chimpanzee. Another similar ape was discovered in the Miocene of Northern Spain in 1913, showing its wide distribution. Other monkey forms of the same age have come to light in Italy and Greece, showing resemblance to the baboons and Langur monkeys, and monkeys representing Cercopithecus have been found in the Pliocene beds of France.

It is clear, therefore, that the reduction in number of the teeth from the full mammalian formula of 44, i.e. I. $\frac{3}{3}$, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3}$, which is characteristic of man and the primates generally, took place at a remote geological epoch. No precise evidence exists as to which teeth have been lost. In the lower orders of mammals, premolars are usually lost from the front of the series, and it is therefore assumed that it is P. 1 and P. 2 which have disappeared from the teeth of man and the apes. The missing incisor is more difficult to define. Analogy with the lower animals points to I. 3, but indications are not wanting that it is I. 2. Thus, in cases of alveolar hare-lip, the cleft usually runs between the central and lateral teeth. Not infrequently a third incisor appears to the mesial side of the cleft which, if it really represents man's lost incisor, indicates I. 2 as the real homology of that tooth.

Differences in the Jaws and Teeth of Anthropoid Apes and Man

Anthropoid Apes	*Man*
1. Jaws and teeth, large.	1. Jaws and teeth, small.
2. Mandible, with short, squarish, broad rami, transverse condyles, narrow, shallow sigmoid notch.	2. Mandible, with narrow, thin, elongated rami, deep sigmoid notch, condyles oblique and rounded.
Alveoli, stout and thick. Much roughened for attachment of muscles.	Body of jaw, slender.
Absence of chin.	Chin, well developed.
Pit and shelf of bone at symphysis for attachment of tongue.	Tubercles at symphysis, for attachment of tongue.
Glenoid cavity, flattened.	Glenoid cavity, deep and concave.
Movement restricted by reason of large canines, limiting lateral action, so that the inner cusps of the molars are worn before the outer; shallow glenoid cavity admitting antero-postero play of the mandible.	Movement, rotary, by reason of rounded condyles, deep glenoid fossa and short canines.
Plane of occlusion, flat.	Plane of occlusion curved.
3. Prognathous.	3. Orthognathous in higher races.
	Prognathous in lower races.
4. Arrangement of teeth, squarish in front, in parallel lines behind. Converging at the back.	4. Arrangement of teeth, in sweeping curve, wide at the back.
5. Incisors, huge square crowns, very stout, and broad at the base; in the orang-outang the lower central incisors are wider than the laterals.	5. Incisors slender. Lower centrals smallest.

Anthropoid Apes	*Man*
6. Canines, large and powerful. Sexual weapons in the male erupting after m. 3; in the female smaller, and erupting after m.2.	6. Canines small, not raised. No sexual difference; erupt before m. 2.
7. Premolars, larger in proportion: crown of lower p.1 bent inwards in orang-outang: upper premolars three-rooted, lower, two-rooted.	7. Premolars, single rooted, except p.1, which sometimes bifurcates, and occasionally is three-rooted.
8. Molars, increase in size towards the back of the mouth, except with chimpanzee; crowns large, square, with well-pronounced patterns, and large cusps; roots long and divergent.	8. Molars, decrease in size, upper crowns similar patterns, but in last molars cusps tend to coalesce and roots to become fused.
9. Intermaxillary bone large, premaxillary suture open throughout life, except in chimpanzee, where it closes after eruption of the permanent canine.	9. Intermaxillary bone small; premaxillary suture closes at birth.
10. Diastema in upper jaw.	10. No diastema.

Palæolithic Man

Numerous illustrations have been brought to light during the last half century of the remains of primitive humanity, showing striking differences in the jaws and teeth from those of modern man.

Pithecanthropus.—In 1891, Dr. Eugene Dubois unearthed in early Pleistocene gravels at Trinil, in Java, a skull cap, femur and three teeth, a premolar and two molars.

The cranial capacity was thought to be about half the dimensions of the average modern man, and the skull cap suggests a being more simian than human in appearance.

The upper molar teeth are of primitive appearance, the crowns large, wide and bulbous on the distal surfaces, each three-rooted, the two buccal roots being fused.

The evidence points to a being with simian and human affinities.

Heidelberg Man.—In 1908 Dr. Shœtensack discovered in the gravels of the river Neckar, near Heidelberg, a human mandible, unique in appearance.

Fig. 251.—Half lower jaw (Heidelberg).

It was found at a depth of 80 feet from the surface in deposits of early Pleistocene date.

The specimen was of great size, very massive, twice the thickness of the modern mandible, and of uncommon breadth.

It had a short and square ramus, shallow sigmoid notch,

Fig. 252.—Lower jaw of Chimpanzee.

and low condyles ; the bone behind the molars was thickened enormously for the insertion of the temporal muscles.

In most of its characteristics it was akin to the anthropoids, especially in the absence of a chin, but the teeth were arranged in a broad sweeping curve, all on the same level, without

interspaces, the first and second molars were of equal size, and the pulp chambers were unusually large. It was a jaw unlike anything ever seen before, with Simian and human relations.

Eoanthropus Dawsonii—Piltdown Man.—Our knowledge of primitive humanity has been further enriched by the discovery of human remains by the late Mr. Charles Dawson, at Piltdown, in Sussex, in 1912.

They consisted of fragments of a skull and portion of a mandible, embedded in gravels, thought to be of early Pleistocene date.

The fragments were twice the thickness of the skull of modern man. A restoration has shown that the cranium was of ordinary capacity, but ill-developed in front, the forehead being low and narrow. The right side of the mandible is simian in character, with a short, stout, square ramus, shallow sigmoid notch, and entire absence of chin, while at the symphysis, internally, the bone is projected into a flange, as in apes.

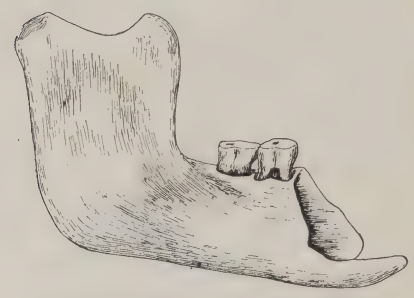


FIG. 253.—Portion of lower jaw (Piltdown).

The tongue was attached in front to a pit, as in the anthropoids, instead of to tubercles, as in man.

The only teeth present are the first and second molars, both quinque-cuspid and much worn on the surface, showing that there was considerable lateral movement of the jaws, and suggesting small canines.

In September, 1913, a lower canine was found in the same place resembling the deciduous canine of an ape, much worn on the lingual surface.

The jaw was simian, but the molars were human in pattern.

Neanderthal Man.—Numerous examples of this remarkable race have been found in limestone caverns at Neanderthal, Germany, Spy, Belgium, and from the Dordogne district of France, the remains of cave dwellers who resided there during the Glacial period.

The many crania and jaws brought to light show skulls with large cranial capacity, but deficient in the frontal region.

The orbits were huge and round, encroaching on the forehead, with gorilla-like supra-orbital ridges, which must have given the creature a savage appearance.

The jaws were prognathous, the mandible massive and of great depth, and the chin was absent. The molars increased in size from the first to the third. The pulp chambers were remarkably large, extending far below the alveolar border, and the roots were diminutive, giving to the tooth a hypsodont appearance.

This race of Neanderthal became extinct in Europe about the middle of the Pleistocene. Professor Sir Arthur Keith considers that Neanderthal man was not the Pleistocene ancestor of the modern man.

Aurignacian Man.—Towards the end of the Glacial period another race of men appeared in Southern Europe, the Aurignacian hunters, who have left such wonderful examples of their art in caves in central and southern France and northern Spain, where the lifelike paintings of the animals with whom they were associated, and the splendid carvings on bone, horn and ivory, testify to their extraordinary artistic skill. The skulls of Aurignacian man demonstrate an intelligent race with large brains, and with jaws and teeth similar to our own. All Simian characters had disappeared, and the type of modern man had arrived.

When man first made his appearance his skull, jaws and teeth still retained many simian characteristics, proclaiming the lines of his ancestry, and suggesting that he, with his cousins the anthropoid apes, branched off at a very early period from the ancestral primate stem.

The adoption of the erect attitude led to the perfecting of the hand, that marvellous piece of mechanism by which man's progress became assured, and in consequence of this came the increase in cranial capacity and intellectual development.

Instead of great fangs for tearing his prey and fighting his enemies, man had learned to fashion weapons for the protection of his kind, and as instruments of the chase to procure food. It was the perfecting of his hands and the development of his brain that assured man's pre-eminence among the

primates, and this reacted on his whole body, and especially left their mark upon his jaws and teeth.

Instead of the simple movement of opening and closing the jaws, and interlocking of the canines, as in the apes, the reduction of the points of the latter to the level of the other teeth made a rotary movement possible, and the arrangement of the teeth in a curve, as in the Heidelberg jaw, resulted.

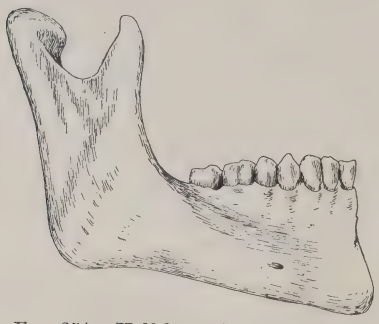


Fig. 254.—Half lower jaw (human).

The widening of the mandible supplied room for the freer movement of the tongue, assisting articulate speech; the pit-like attachment of the tongue, as in the apes, gave place to the attachment to the genial tubercles in modern man. (Fig. 254.)

The modification of the jaw in front, resulting from the adoption of the erect attitude, and the changes in the dentition, ultimately produced the chin. The stages in evolution are clearly seen in the Heidelberg, Piltdown, and Neanderthal specimens.

Changes in the Jaws and Teeth of Modern Man

Numerous pre-Christian burial grounds of the early Saxons, who penetrated into Mercia in the sixth century, exist in the river valleys of central England.

The skulls are magnificent and the jaws and teeth show perfect dentitions, arranged in sweeping curves, with no tendency to crowding and little sign of caries. The patterns of the crowns are ideal and the roots of the molars are all separate.

In examining the teeth of modern man one is impressed with the great changes which have taken place even in recent historical time.

The tendency of the jaws of civilized races is to contract into a narrower arch, causing irregularities in the front teeth and a tendency to a reduction in size of the upper lateral incisors. These are often small conical teeth, and we not

infrequently find suppression of one or both of the lateral incisors.

The same thing applies to the third upper molar which, as we have just noticed, in numerous instances is reduced to a rudimentary cone, and is often entirely absent; these changes have doubtless been the result of altered food, habit and environment.

Taking the English race as an example, since mediæval times, when the occlusion of the incisors was often edge to edge, the character of the food has completely altered.

Then the staple food of the masses was coarse rye bread or a mixture of wheat, barley and rye; wheat was at first only a food for the rich, and contained much of the chaffy husks with the phosphate of lime so necessary for building up the bones and teeth.

Beer made from barley and wheat formed the drink of the masses of the people, its purity was controlled by the Assize Courts, and ale tasters were appointed by the Court Leet.

Voyages to the East Indies and the discovery of America in the fifteenth and sixteenth centuries introduced food of quite a new character, and by the end of Elizabeth's reign potatoes had been imported from the West Indies and were fast coming into favour. Coffee and tea came to England in the middle of the seventeenth century, and by Queen Anne's reign coffee houses were established throughout London.

In the eighteenth century tea gradually supplanted ale at the tables of the well-to-do, and has now become the beverage of the masses.

Greater facilities in navigation have brought abundant supplies of rice from the Far East and maize from North America, while sugar from the West Indies has supplied a valuable and universal food for rich and poor alike.

Cranial and Dental Measurements

Perhaps the most noticeable feature in which modern European man differs from the lower races, and in which man as a whole differs from his extinct ancestors, human and simian, is in his reduced prognathism. This is due partly to the increased development of the front part of the cranium, and partly to a diminution in size of the jaws and facial bones

generally. Many attempts have been made to devise measurements which will express the degree of prognathism in different skulls for accurate comparison. Earlier anthropologists devised various formulæ for measuring the facial angle, i.e. the angle made with the horizontal by a straight line running from the forehead to the edge of the upper incisor teeth. Such formulæ are, however, apt to be invalidated by unimportant differences in the development of the supra-orbital ridges, or in the forward inclination of the incisors; and the anthropological measurement most widely used to-day, to express the degree of prognathism, is that known as the *gnathic index*. To obtain this, two lines are measured on the skull by calipers, one from the basion (the middle of the front margin of the occipital foramen) to the nasion (the naso-frontal suture), the line being known as the basio-nasal length; the other from the basion to the front edge of the upper alveolus between the two central incisors, this being called the basi-alveolar length.

The formula is as follows:—

$$\text{gnathic index} = \frac{\text{basi-alveolar length} \times 100}{\text{basio-nasal length.}}$$

Skulls are classified as orthognathous when the index is below 98; mesognathous when it is between 98 and 103; and prognathous when it is above 103.

Modern European white man differs from the races of other continents, not only in his reduced prognathism, but by possessing teeth which are relatively small compared with the size of his skull.

The feature is of interest for anthropological comparison, and has been reduced to a formula known as the *dental index*. Two lines are taken, one from the front of the first premolar and the back of the third molar measured *in situ*, the other the basio-nasal length, as already described.

The formula is as follows:—

$$\text{Dental index} = \frac{\text{length of teeth } 100}{\text{basio-nasal length.}}$$

Microdont races of Europeans, Egyptians and Polynesians have a dental index of 42. For Mesodont races of Chinese, Negroes, Malays and American Indians, the figure is 43; while Megadont races of Australian and Tasmanian blacks have a dental index of 44 and over.

GLOSSARY

Acrodont. Teeth anchylosed by their base to the summit of the bone of attachment.

Analogy. Similarity in function, but not necessarily in origin.

Anchylosis. Fixed attachment to the bone by calcified tissue, as in teeth of many fishes.

Brachyodont. Molar crowns short, with distinct roots.

Bunodont. Molar crowns with blunt rounded cusps.

Calcospherite. Globular forms by union of mucilage and lime salts.

Calcoglobulin. Albumen modified by union with salts of lime.

Cingulum. Basal ridge of enamel around neck of tooth.

Collagen. Organic matrix of bone and teeth.

Diastema. Space between teeth.

Diphyodont. Development of two sets of teeth.

Eoanthropus. Piltdown Man.

Eocene. First division of the Cainozoic period, the dawn of the age of mammals.

Eozoic. Upper Archæan division of geological time.

Eutheria. Highest division of placental mammals.

Gnathic. Appertaining to the jaws.

Gomphosis. Socketed as applied to teeth.

Gubernaculum. Fibrous cord attached to apex of tooth sac.

Gymnodont. Naked tooth, a family of fishes.

Heterodont. A dentition in which the teeth vary in shape.

Homodont. A dentition in which all the teeth have the same shape.

Homology. Similarity of origin, though not of function.

Haplodont. Conical crown with single root.

Hypsodont. Teeth with long crowns and short roots, as in horse.

Jurassic. Geological period immediately before the Cretaceous.

Lophodont. Ridged crown, as in rhinoceros.

Mesozoic. Middle period of geological time.

Monotremata. The Prototheria, the lowest or egg-laying division of the mammalia, as Platypus.

Monophyodont. Having only one set of teeth, as Armadillo.

Marsupialia. The metatheria, pouched animals, as Kangaroo.

Miocene. Division of the Cainozoic period.

Oligocene. Division of the Cainozoic period.

Palæontology. Study of extinct life.

Palæozoic. The primary division of geological time.

Polyphyodont. An unlimited succession of teeth, as in fishes.

Pleurodont. Anchylosis of the teeth to the jaw by their sides, as Monitor Lizard.

Pleistocene. Quaternary division of geological time, including the Glacial Period.

Pliocene. The last division of the Tertiary geological epoch.

Ruminant. Animals which chew the cud, e.g. camel, deer, sheep.

Rostrum. Beak-like projection in upper jaw, carrying teeth, as in sawfish.

Selenodont. Crescentic ridged molars, as in ruminants.

Setiform. Hair-like teeth, as in catfish.

Triconodont. Crown with three tubercles arranged in line.

Tritubercular. Crown with three cusps arranged in a triangle.

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